ECOLOGY

Vol. 35 JULY, 1954 No. 3

THE HYDROBIOLOGY OF ATWOOD LAKE, A FLOOD-CONTROL RESERVOIR[1]

JOHN C. WRIGHT
Department of Botany and Bacteriology, Montana State College, Bozeman, Montana

ATWOOD LAKE

This paper contains the results of a two-year investigation of the physical, chemical, and biological characteristics of Atwood Lake, with special reference to the effect of these factors upon the production of desirable crops of game fish.

Financial support for this investigation was provided by the Ohio Division of Conservation in the form of a fellowship, "The Ohio Reservoir Fisheries Research Fellowship," which was set up with the Ohio State University. Dr. T. H. Langlois, Director of the Franz Theodore Stone Institute of Hydrobiology of the Ohio State University at Put-in-Bay, Ohio, was in charge of the supervision and direction of the work.

Atwood Lake, one of several flood-control reservoirs of the Muskingum Watershed Conservancy District, failed to produce satisfactory fish crops since impoundment in 1939. Because a high carp population was present and the water was "murky," the hypothesis was advanced that the carp, by virtue of their feeding habits, were making the lake turbid, thus creating an unfavorable biotic situation for game fish. Consequently, in the fall of 1946, the lake was drained in an effort to eliminate the carp. Upon refilling, it was restocked with desirable fish. The author's problem was to evaluate the effect of drainage and carp removal upon the limnology of the lake, to determine whether biotic competition of carp, or some other factor or factors, was responsible for the poor game-fish production. Unfortunately, carp and other undersirable fish gained entrance following drainage.

Atwood is an artificial lake created by the damning of Indian Fork Creek. The earthen dam was completed September 23, 1937 by the Corps of Army Engineers. At conservation pool level, the reservoir has a capacity of 23,600 acre feet and a surface area of 1,540 acres. The maximum depth at this level is 37 feet (11.2 m), and the average depth is 15.3 feet (4.6 m). The outlet gates are located in the old channel of Indian Fork Creek. Drainage is controlled by gates and siphons in the bottom of the gate house.

At the completion of the dam in 1937, the basin was grubbed of vegetation. From then until the lake was partially filled in 1939, native brush was allowed to grow. The water level was kept at a maximum of 23 feet in order to carry on road relocation in the basin until October 14, 1946 when the lake was drained. On February 1, 1947, it was refilled and brought up to conservation pool level, a rise of 14 feet. For the first time about 730 acres of land, most of which was covered with second-growth brush, were flooded.

The watershed comprises an area of 70.3 sq. mi. lying almost wholly in Carroll County, Ohio. This region is situated in a highly dissected peneplain which makes up part of the unglaciated Allegheny Plateau. The underlying rocks are largely shales and sandstones with interbedded coal seams. No large limestone exposures occur. The majority of the soils are classified as Muskingum silt loam. They are acid, ranging in pH from 6.7 to 4.5, and they are low in replaceable potassium, phosphorus, and calcium. The lack of basic fertility, coupled with improper land practices on the steep hillsides, has resulted in an average topsoil loss of 59.3% (Morse 1939).

METHODS

Collections and limnological measurements were made at intervals at five stations, the locations of which are shown on the map of Atwood Lake (Fig. 1). All temperature determinations were made with a Negretti and Zambra reversing thermometer at depth intervals of one meter at Station 5. Transparency was measured by means of a standard Secchi disc. Turbidity was determined by two methods. For turbidities greater than 25 ppm., the Jackson turbidimeter was used; for turbidities less than 25 ppm., the visual comparator of Weeks and Chandler was employed (Weeks and Chandler 1945). The United States Geological Survey colorimeter was used to measure color. Light penetration was measured with a Weston photometer, similar to the one described by Atkins *et al.* (1938), mounted in a watertight case.

Water samples for all chemical analyses were

[1] A thesis presented to the Graduate School, the Ohio State University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Hydrobiology. Contribution of the Franz Theodore Stone Institute of Hydrobiology.

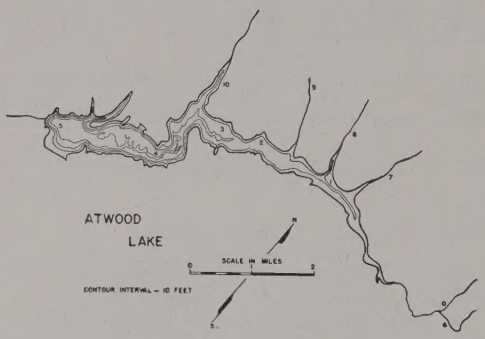

FIG. 1. Map of Atwood Lake showing depth contours and location of lake and stream sampling stations.

collected with a modified Kemmerer water bottle. Hydrogen-ion concentration was measured with La Motte colorimetric standards. Dissolved oxygen, total alkalinity, nitrites, nitrates, ammonia, phosphates, total iron, and oxygen consumed were determined by methods outlined in the Standard Methods of Water Analysis, ninth edition, 1946.

Plankton samples were collected at the surface at all stations and at the surface, two, four, and six meter depths at Station 5 with a Kemmerer water bottle. The contents of the bottle (2.15 liters) were filtered through a Birge and Juday plankton bucket. The samples were preserved with formaldehyde and concentrated to 10 ml. with a pipette covered at the lower end with number 25 silk bolting cloth. One ml. of the thoroughly mixed sample was transferred to a Sedgewick-Rafter cell and the phytoplankton was counted. Abundant forms, i.e. over 20,000 per liter, were enumerated by counting twenty fields covered by a Whipple micrometer and multiplying the total number by the proper factor. All of the less abundantly occurring forms were counted on the entire slide and converted to numbers per liter. All of the zooplankton forms on the slide and in the remaining nine ml. were counted. Bottom samples were collected with an Ekman dredge at several locations in a series; the number of organisms was counted.

The photosynthetic rates of the phytoplankton were determined by suspending from a float into the lake a clear and a black 8-oz. glass-stoppered bottle. Each bottle contained lake water taken from the depths, surface, two, four, six, and eight meters, at which the bottles were to be suspended. The amount of dissolved oxygen was determined at the start of the experiment. The bottles were removed from the lake at the end of 48 hours, and the dissolved oxygen in the bottles was determined. The difference in oxygen concentration between the black and white bottles was taken as a measure of the gross photosynthetic activity of the phytoplankton. The decline in oxygen concentration between the original oxygen concentration and that of the black bottle was a measure of respiration of the plant, animal, and bacterial populations.

In addition to samples taken from the lake itself, measurements of turbidity, hydrogen-ion concentration, total alkalinity, nitrates, nitrites, and phosphates were made for water samples of the six major tributaries, Stations, 0, 6, 7, 8, 9, and 10 (Fig. 1).

PHYSICAL DATA

Temperature. Temperature records taken at Station 5 are presented in Figure 2. The variations of temperature can be divided into four temperature seasons: fall overturn, period of ice cover, spring period of uniform temperatures, and summer stagnation.

The fall overturn occurred between September 12 and October 5, 1947, September 1 and October 11, 1948, and September 1 to September 3, 1949.

Ice cover formed December 1 in 1947 and was still present February 12, 1948. The exact date of ice disappearance is not known. Ice formed December 27, 1948, was still present February 6, 1949, and had disappeared by February 27, 1949.

Vertical differences in temperatures were first observed on April 27, 1948 when the surface temperature of 17.8° C. exceeded the temperature at eight meters by 4.7° C. As a result of cooler weather, the lake was practically thermally homogeneous until June 3, at which time thermal stratification was established. Due to this stratification, the rise in temperature at and below the six meter level was very slow and averaged only 4° C. from June 3 to September 1.

Temperature homogeneity existed from October 11 to May 2, 1949. On May 6, a definite thermocline was established between the five and six meter levels. As a result of cool weather between July 16 and 25, there was almost complete vertical circulation between the surface and eight-meter stratum. An average gain in temperature of 4° C. occurred in the six to eight meter layer of water between July 16 and 25 compared to a gain of 2.2° C. between June 9 and July 16.

Transparency. Maximum, minimum, and average values for the depth at which the Secchi disc disappeared at the various lake stations are given in Table I. Transparency was lowest at Station 1 and increased successively down the lake to Station 5. The average values for transparency were greater for all stations except Station 5 in 1949 than in 1948. Analysis of the probable significance of these differences by Fisher's (1934) "method of *t*" showed that there was less than

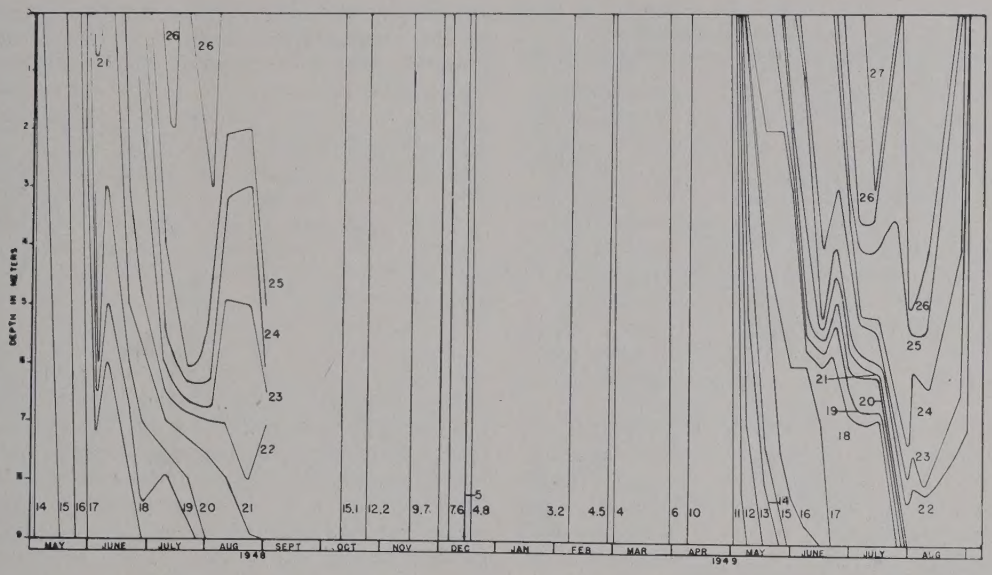

FIG. 2. Depth distribution of temperature isotherms, °C.

TABLE I. *Maximum, Minimum, and Average Values of Transparency (Expressed as meters depth at which the Secchi disc disappeared)*

	Station	1	2	3	4	5
1948	Maximum.....	1.3	1.5	2.0	2.2	2.0
	Minimum.....	.1	.1	.2	.3	1.2
	Average.....	.6	1.0	1.1	1.4	1.7
1949	Maximum.....	1.0	1.9	2.0	2.6	2.5
	Minimum.....	.3	.6	.5	.7	1.3
	Average.....	.8	1.3	1.4	1.6	1.6

one chance in twenty of drawing samples yielding differences as great as these from a homogeneous water mass. Most of the variation was between the spring months of the two years.

Average turbidity was as follows: Station 1, 21 ppm., Station 2, 17 ppm., Station 3, 13 ppm., Station 4, 9 ppm., and Station 5, 7 ppm. Maximum turbidity was: Station 1, 100 ppm., Station 2, 120 ppm., Station 3, 80 ppm., Station 4, 35 ppm., and Station 5, 25 ppm. These values were recorded during periods of heavy rainfall in the spring of 1948 when flood-swollen streams carried heavy silt loads into the lake. Only the upper end of the lake was affected markedly by silt, and upon cessation of heavy runoff, the water cleared quickly.

Color at the surface of all stations averaged as follows: Station 1, 40 ppm., Station 2, 27 ppm., Station 3, 21 ppm., Station 4, 16 ppm., and Station 5, 16 ppm. The color of the water from the bottom of the lake at Station 5 increased during stagnation, June 3 to September 1, 1948, from 10 ppm. to 79 ppm. Following fall overturn, color-producing substances were distributed throughout the depth of the lake at Station 5 and averaged 27 ppm. on October 11, 1948. In contrast to turbidity, color remained high throughout the summer at Stations 1 and 2 and to a lesser extent at Station 3. These stations were located in the area of the lake where large tracts of brush and trees were submerged for the first time in 1947.

A series of 15 analyses of color, total iron, and organic content of the water was made in order to determine if total iron and organic matter were correlated with color. Upon oxidation with hot potassium permanganate solution, the oxygen-consuming power of the water was taken as a measure of organic content. Correlation analyses were made using these data and the results are shown in Table II. Although the simple correlation coefficients between color, oxygen consumed, and total iron were significant, partial correlation coefficients between color and total iron and between color and oxygen consumed were not. This may be interpreted to mean that the oxygen-consuming power of the water and total iron were not independent variables but combined their effects in producing color. This conclusion is strengthened by the highly significant and greater value of the multiple correlation coefficient of color with oxygen consumed and total iron.

In order to determine the relative effects of color and turbidity on transparency, correlation analyses, utilizing a series of 40 simultaneous determinations of transparency, color, and turbidity,

TABLE II. *Correlation Coefficients between Color, Total Iron, and Oxygen Consumed*

Variables	Correlation Coefficients
Color with total iron	r = .693**
Color with oxygen consumed	r = .686**
Total iron with oxygen consumed	r = .609*
Color with total iron when oxygen consumed is constant	r = .455
Color with oxygen consumed when total iron is constant	r = .477
Color with total iron and oxygen consumed	R = .771**

*Significant to the 5% level of probability.
**Significant to the 1% level of probability.

TABLE III. *Correlation Coefficients between Transparency, Color, and Turbidity*

Variables	Correlation Coefficients
Transparency with turbidity	r = −.454**
Transparency with color	r = −.701**
Turbidity with color	r = .348*
Transparency with turbidity, when color is constant	r = −.318*
Transparency with color, when turbidity is constant	r = −.677**
Turbidity with color, when transparency is constant	r = .047
Transparency with turbidity and color	R = −.735**

*Significant to the 5% level of probability.
**Significant to the 1% level of probability.

were made. The results are given in Table III. Since the partial correlation coefficient between color and turbidity was insignificant, it may be concluded that there was no interaction between the two variables. The significant correlation coefficient between color and turbidity can be explained by the fact that the highest turbidities and highest color values were present at the upper end of the lake and the lowest turbidities and color values at the lower end. The multiple correlation coefficient between transparency, color, and turbidity was —0.735. Since the partial coefficient between color and transparency was greater than that between turbidity and transparency, it can be concluded that color was the chief factor affecting light penetration except during periods when heavy rainfall resulted in appreciable amounts of siltation in the upper end of the lake.

In order to evaluate the effect of light absorption on the photosynthesis of aquatic plants, the depth at which the compensation point was reached was determined at Stations 1, 2, 3, and 5. The technique of Meyer and Heritage (1941) was followed. *Myriophyllum exalbescens* was used as the test plant because it was the most common submerged aquatic plant in the lake. The effect of color in absorbing incident radiation may be seen by comparing the depth at which the compensation point was reached at the different stations (Table IV).

TABLE IV. *Color, Depth of Compensation Point, and Relative Light Intensity at Compensation Point Depth*

Station	Color (ppm.)	Depth (meters)	Light Intensity (% of incident light)
1	40	2	1.4
2	28	3	3.5
3	24	4	2.4
5	15	6	3.9

The maximum depths at which plants were growing in the lake did not exceed the compensation-point depths since no rooted aquatics were found growing at depths where the light intensity was less than 1.9%. Unfortunately, the upper end of the lake, where most of the shoal areas existed, was the most highly colored, whereas in the lower end of the lake, where the water was more transparent, there was less area available for aquatic plants because of the abrupt drop-off of the lake bottom.

CHEMICAL DATA

Oxygen. From April 8, 1949 to September 3, 1949, vertical series of oxygen determinations were made at Station 5 at two-meter intervals. The ranges of oxygen concentration were: surface, 10.70 to 5.24 ppm., two meters, 10.90 to 4.34 ppm., four meters, 10.56 to 3.26 ppm., six meters, 10.54 to 0.66 ppm., and at eight meters, 10.44 to 0.28 ppm.

Supersaturation was observed on two dates; July 11, when excess oxygen ranged from 0.40 ppm. at the surface to 0.50 ppm. at the four meter level and on August 12 when an excess of 1.19 ppm. was present at the surface and 0.69 ppm. excess at the two-meter level. Supersaturation on these dates was correlated with major phytoplankton pulses.

Actual oxygen deficits ranged from 0.07 to 3.14 ppm. at the surface, 0.17 to 4.04 ppm. at two meters, 0.68 to 5.27 ppm. at four meters, 0.79 to 7.72 ppm. at six meters, and 0.89 to 9.30 ppm. at eight meters. On the whole, oxygen concentrations indicated an ascendancy of oxygen-consuming processes over photosynthesis.

Total Alkalinity and pH. Average total alkalinity at Station 1 was 50.5 ppm., Station 2, 39.4 ppm., Station 3, 34.1 ppm., Station 4, 31.9 ppm., Station 5, 31.6 ppm. The decrease in total alkalinity down the lake was due in part, at least, to the presence of coal mine dumps and acid-bearing

iron springs in the bottom of the lake and mine waste pollution in the stream on which Station 10 was located. Fluctuations in total alkalinity ranged from 96.8 to 16.2 ppm. at Station 1 and decreased in amplitude down the lake to Station 5 where the range was 48.4 to 24.5 ppm. The higher values were recorded in the summer when stream flow was at a minimum and the lower values in the spring as a result of the dilution of ground water discharge by heavy surface runoff.

The range of pH was 6.0 to 7.4 at Station 1 and 6.2 to 7.6 at Station 5. The pH of the lake water generally followed that of incoming water.

Inorganic Nutrients. The concentration of inorganic nitrogen compounds, ammonia, nitrites, nitrates, in the tributary streams of Atwood Lake was very low; Station 0, 0.03-0.10 ppm., Station 6, 0.10-0.57 ppm., Station 7, 0.02-0.08 ppm., Station 8, 0.03-0.06 ppm., Station 9, 0.04-0.07 ppm. The higher concentration of ammonia (0.04-0.10 ppm.) and nitrites (0.06-0.47 ppm.) in Indian Fork Creek (Station 6) was caused by the inflow of sewage plant effluents at Carrollton which is located 13 miles upstream from the lake.

In the lake itself, total inorganic nitrogen ranged from 0.03-1.05 ppm. at both the surface and bottom. Ammonia ranged from 0.00-0.06 ppm. at the surface and from 0.00-0.60 ppm. at the bottom, nitrites from 0.001-0.04 ppm. at the surface and 0.01-0.17 ppm. at the bottom, and nitrates from 0.00-1.00 ppm. at both the surface and bottom.

Soluble phosphates were detected at the surface only once (0.001 ppm.) in a series of 13 chemical analyses. In the bottom waters of the lake, soluble phosphates were present in a concentration of 0.005 ppm. on September 1, 1948. At all other times, it was undetectable. Mortimer (1941) and Hutchinson (1941) have shown that phosphates are adsorbed by the oxidized mud-water interface at the lake bottom when the supernatant water is uniformly oxygenated. With the decline of oxygen following thermal stratification, the mud-water interface becomes reduced and releases adsorbed ions to the water. This phenomenon accounts for the appearance of phosphate ions in detectable quantities at the bottom of Station 5 during stagnation. A large part of the ions released in this manner would be lost through the outlet channel since the lake drains from the bottom. Pearsall *et al.* (1946) recommend that water supply reservoirs be constructed so that compensation water can be drawn from below the thermocline during the summer and thus deplete the reservoir of nutrients in order to decrease the growth of phytoplankton. In this respect, Atwood Lake was a very inefficient accumulator of mineral salts necessary to sustain organic production upon which a fish population is ultimately dependent.

It is anomalous that soluble phosphates could not be detected in the lake itself, when the concentrations of soluble phosphates recorded at Station 6 on Indian Fork Creek ranged from 0.005-0.340 ppm. It is apparent that something happened to the soluble phosphorus between Station 6 and the lake. Therefore samples of water were taken at a series of stations between the sewer outlet at Carrollton and Station 1. Soluble phosphorus averaged 0.477 ppm. at Carrollton, decreased steadily downstream, and was undetectable at Station 1.

Phytoplankton

General features of seasonal distribution and relative abundance of phytoplankton are shown in Figure 3 and Table V. Phytoplankton numbers from the periods April 14 to September 1, 1948 and March 25 to August 3, 1949 are averages of surface plankton collected from all five lake sampling stations. For the period October 13, 1948 to February 27, 1949, the populations at Station 1 and 5 were averaged. The last three collecting dates, August 15 to September 3, 1949, are based on the results of collections at Station 5. All references to phytoplankton populations are based on this method of computation unless the population of a particular station is specified.

Table V. *Average Spring, Summer, Fall and Winter Phytoplankton Populations (cells or colonies per liter)*

	1948		1948-1949	1949	
	Spring	Summer	Fall and Winter	Spring	Summer
Bacillarieae	11,850	196	507	3,996	3,304
Chlorophyceae	24	760	216	765	143,262
Chrysophyceae	4,279	2,006	181	2,088	668
Dinophyceae	6	89	2	2	3
Euglenophyceae	79	128	59	564	3,185
Myxophyceae	0	775	53	151	26,070
Total Phytoplankton	16,238	3,954	1,018	7,566	176,492

The highest population in 1948 was 36,465 cells per liter and occurred on April 14. Diatoms, mostly Asterionella and Diatoma, made up 91% of the population at this time. The phytoplankton declined after this date, reaching a low of 1,027 cells or colonies per liter on May 24, and then rose to a peak of 11,653 individuals per liter on June 12. Of the population on this date, 83% was Chrysophyceae, largely Dinobryon. The drop in numbers to a low of 1,417 cells per liter on July 11 was due largely to a decline of Chrysophyceae. A further rise in numbers on July 11

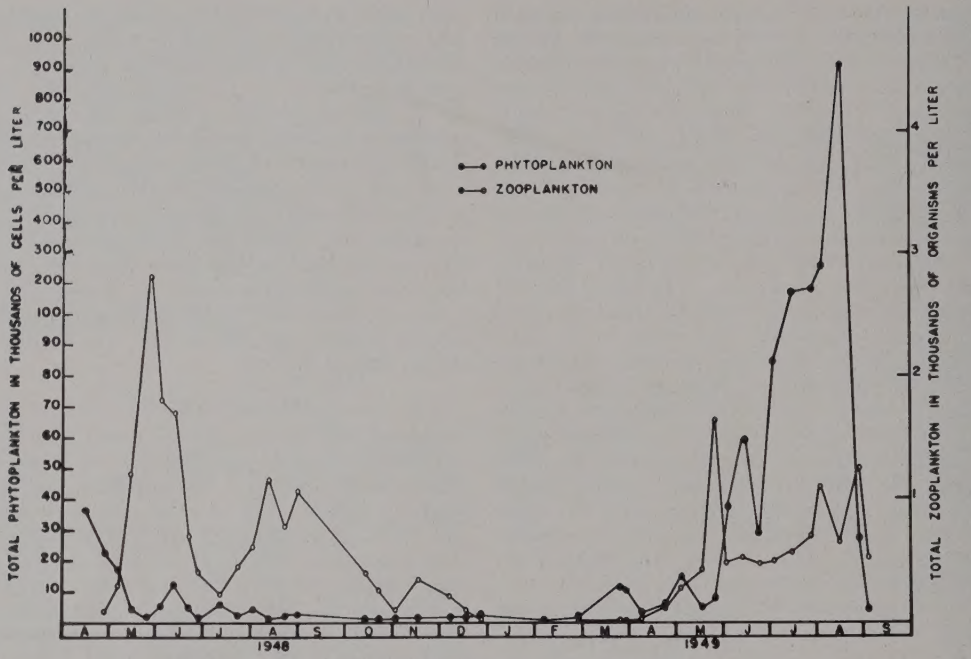

FIG. 3. Total phytoplankton and total zooplankton.

to 6,023 cells per liter was due to another pulse of Dinobryon which upon decline brought about a population low of 2,111 cells on July 22. The rise in total phytoplankton to 3,001 on August 2 was due to an increase of green algae which made up 83% of the population on this date. Coelastrum and Scenedesmus were the most important genera. Total phytoplankton then declined as a result of a decrease in green algae. This decline was followed by a buildup of blue-green algae, mostly Chroococcus, which caused the slight rise from August 12 to September 1. Blue greens made up 65% of the population on September 1.

Total phytoplankton was not observed to exceed 1,400 cells per liter during the period October 13, 1947 to February 27, 1948. Diatoms were the dominant form, making up 80% of the population. The next most abundant algae were the Chrysophyceae, mostly Synura, which varied from 3 to 40% of the population and reached a midwinter maximum of 544 on December 27. Chlorophyceae declined steadily in numbers during the period from 510 (40%) on October 13 to 0 on February 6.

The two phytoplankton pulses that occurred on March 25 and June 13, 1949 and which reached respective maximums of 10,127 and 59,192 cells per liter were due largely to the diatoms, Asterionella and Diatoma. After June 13, the diatoms rapidly decreased. The rise in total phytoplankton following June 23, 1949 was due in large part to an increase in green algae, which reached a maximum on August 15 when they made up the most important group. Quadringula was the most important genus. The blue-green algae, largely Coelosphaerium, reaching a maximum of 130,759 (77%) cells per liter on July 14, made up a smaller part of this increase. Following the August 15 maximum, total phytoplankton rapidly declined.

Marked differences in horizontal distribution of phytoplankton were noted (Table VI). Total phytoplankton was lowest at Station 2 both years and gradually increased down the lake to Station 5. Bacillarieae and Chlorophyceae followed this same pattern, while Chrysophyceae and Euglenophyceae were in greatest number at Station 1 and exhibited a decreasing trend down the lake to Station 5. Populations of Myxophyceae were not significantly different at the five stations in 1948 but increased from Station 1 to Station 5 in 1949.

Phytoplankton was much greater in 1949 than in 1948. Average total phytoplankton in 1949 was approximately ten times that of 1948 at Stations 2, 3, 4, and 5 and five times as great at Station 1. It is apparent from an examination of Table V that the variation between years of populations

TABLE VI. *Maximum, minimum, and average populations (cells or colonies per liter) of phytoplankton at each station for the periods April 14-August 2, 1948, and April 8-August 3, 1949*

		Station 1	Station 2	Station 3	Station 4	Station 5
Bacillarieae						
Maximum	1948	4,225	6,012	15,431	70,408	80,140
	1949	16,440	12,020	26,220	24,540	31,700
Minimum	1948	0	0	9	0	20
	1949	0	0	0	0	20
Average	1948	1,382	1,339	2,886	6,535	12,313
	1949	4,397	3,359	3,380	4,107	4,193
Chlorophyceae						
Maximum	1948	2,415	2,497	3,171	5,668	3,458
	1949	88,901	94,440	247,497	442,511	510,681
Minimum	1948	8	16	4	2	2
	1949	31	220	15	15	16
Average	1948	504	366	629	705	675
	1949	43,202	18,889	28,679	48,689	74,244
Chrysophyceae						
Maximum	1948	56,512	20,120	12,416	9,100	378
	1949	18,380	16,130	11,302	6,450	3,280
Minimum	1948	26	0	0	0	0
	1949	0	0	0	0	0
Average	1948	12,662	2,395	2,728	956	62
	1949	3,038	2,175	1,421	959	441
Euglenophyceae						
Maximum	1948	1,646	369	130	55	57
	1949	38,300	7,670	1,741	520	800
Minimum	1948	0	2	0	0	0
	1949	4	0	0	0	0
Average	1948	394	118	45	8	20
	1949	11,550	1,657	340	283	156
Myzophyceae						
Maximum	1948	4,806	1,170	1,187	2,700	1,604
	1949	26,384	83,500	150,130	235,440	217,740
Minimum	1948	0	0	0	0	0
	1949	0	0	0	0	0
Average	1948	909	577	624	915	550
	1949	10,425	14,100	21,849	32,474	34,511
Average Total Phyto-plankton	1948	15,851	4,795	6,912	9,119	13,620
	1949	72,612	40,180	55,669	86,512	113,545

of those groups which comprise the spring flora, such as diatoms and Chrysophyceae, was not great, but the variation between populations of the summer groups, such as Chlorophyceae, Myxophyceae, and Euglenophyceae, was great. It is the higher populations of the latter groups in 1949 which explain the great variation in total phytoplankton levels between years. Three possible factors can be suggested which may explain this variation.

Heavy rainfall occurred previous to April 14, 1948 and resulted in a rise in water level of five feet in the reservoir. Between April 14 and April 27, this excess of water was drained off. The movement of flood water into the upper end of the lake reversed the normal gradient of total alkalinity (Table VII). With the abatement of the flood, total alkalinity of the upper end of the lake began to rise, closely following the higher alkalinity of tributary streams, while alkalinity values in the lower end of the lake continued to fall as the flood water mass moved down lake, reaching a minimum on May 5 at Stations 4 and 5. With cessation of flood conditions, the rate at which water was received into the lake fell off greatly and consequently the rate at which the stored flood water was replaced in the reservoir was very slow. The total alkalinity at Station 5, for example, did not reach the same concentration it had before the flood until August 2. At the time flood waters were entering (April 14), diatom populations were larger down the lake from Station 1 to Station 5. On April 27, the zone of flood water had moved further down the lake and the diatom population had begun to decline in the lower end. On May 5, Station 5 felt the full effect of the flood and the diatom population was drastically reduced. On May 15, the order of abundance of diatoms between stations became completely reversed from that of April 14. This slowly replaced mass of flood water apparently exerted a depressing effect on phytoplankton throughout the summer of 1948.

TABLE VII. *Diatom Population (cells per liter) Compared to Total Alkalinity (ppm.)*

	Station 1	Station 2	Station 3	Station 4	Station 5
April 14, 1948					
Diatoms	2,817	6,012	15,431	70,408	78,856
Total Alkalinity	16.2	14.9	27.4	31.0	32.0
April 27, 1948					
Diatoms	4,250	3,168	13,666	3,860	60,526
Total Alkalinity	30.0	23.6	22.4	27.0	29.0
May 5, 1948					
Diatoms	4,225	2,475	2,545	3,246	6,005
Total Alkalinity	38.0	33.9	24.8	23.5	24.5
May 15, 1948					
Diatoms	1,738	1,038	569	25	217
Total Alkalinity	37.5	31.5	29.0	25.5	24.5

No such serious flood occurred in the spring of 1949. A high rate of water movement into the reservoir from March 25 to April 5, 1949 apparently brought the March diatom pulse (Fig. 3) to an end, but this rate of water movement was not of sufficient magnitude to completely flush the reservoir as did the April floods of 1948.

Between July 16 and 25, 1949 (Fig. 2), a partial overturn of the lake occurred which meant that mineral nutrients which had accumulated in the hypolimnion now became available to the phytoplankton in the epilimnion. The very great rise in phytoplankton subsequent to July 16 (Fig. 3) followed this event. No such thermal behavior occurred in 1948.

On comparing total phytoplankton and total zooplankton populations (Fig. 3), it will be noted

that the late spring-early summer pulse of zooplankton was accompanied by a phytoplankton minimum. The 1948 zooplankton pulse was much larger and lasted longer than did the 1949 pulse. Furthermore, the cladocerans, which would be expected to exert the greatest grazing pressure, played a much more important role in 1948 than in 1949 (Table VIII). It seems possible that the grazing pressure exerted by the zooplankton had some effect on phytoplankton populations and that the much greater grazing pressure in 1948 as compared to 1949 was one of the factors responsible for the difference in phytoplankton between the two years.

TABLE VIII. *Average Spring, Summer, Fall and Winter Zooplankton Populations (number of organisms per liter)*

	1948		1948-1949	1949	
	Spring	Summer	Fall and Winter	Spring	Summer
Cladocera	17o	147	10	53	51
Copepoda	42	111	22	23	75
Rotifera	734	630	137	o98	544
Protozoa	9	539	102	50	719
Total Zooplankton exclusive of Protozoa	949	888	169	474	670

ZOOPLANKTON

General features of seasonal distribution and relative abundance of zooplankton are shown in Figure 3 and Table VIII. Zooplankton numbers were treated in the same manner as phytoplankton. Zooplankton was at a minimum, 169 organisms per liter, during the fall and winter period. The average number in the spring of 1948 was 949 organisms per liter, and in 1949, 474 per liter. The summer averages were 888 in 1948 compared to 670 per liter in 1949.

Two major pulses were observed both years, a late spring-early summer pulse followed by a midsummer minimum and a late-summer pulse. The late spring-early summer pulse in 1948 was much larger than that of 1949, going from a low of 114 organisms per liter to a maximum of 2,820 organisms per liter on May 24. The percentage composition on this date was 2% Copepoda, 23% Cladocera, and 75% Rotifera. The late summer maximum of 1,163 organisms was reached on August 12, of which 20% was Copepoda, 13% Cladocera, and 67% Rotifera.

In 1949, the number of zooplankton increased from a low of 20 per liter on March 28 to a high of 1,658 per liter on May 25, of which 2% was Copepoda, 7% Cladocera, and 91% Rotifera. A mid-summer low of 452 organisms per liter was reached on June 23, of which 8% was Copepoda, 18% Cladocera, and 74% Rotifera. A late-summer maximum on August 27 of 1,246 organisms per liter was composed of 4% Copepoda, 4% Cladocera, and 92% Rotifera.

The highest population observed during the fall and winter period was 389 organisms per liter on October 13, 1948, of which 17% was Copepoda, 7% Cladocera, and 76% Rotifera. The lowest population, 17 organisms per liter, was found on February 6, 1949, of which 41% was Copepoda, 53% Cladocera, and 6% Rotifera.

Copepoda were most abundant in late summer, reaching a maximum of 230 per liter in 1948 and 178 per liter in 1949. During both years the average populations did not differ greatly between stations (Table IX). The maximum, minimum, and average populations at all stations were greater in 1948 than in 1949. *Cyclops viridus* and *Diaptomus oregonensis* were the most important species present.

TABLE IX. *Maximum, minimum, and average populations (organisms per liter) of zooplankton at each station for the periods April 14-August 2, 1948, and April 8-August 3, 1949*

		Station 1	Station 2	Station 3	Station 4	Station 5
Cladocera						
Maximum	1948	1,739	1,123	344	156	212
	1949	176	168	522	306	43
Minimum	1948	0	1	1	10	3
	1949	0	1	4	4	3
Average	1948	317	234	97	72	48
	1949	62	77	105	82	13
Copepoda						
Maximum	1948	177	391	297	184	138
	1949	100	191	80	122	92
Minimum	1948	1	7	16	15	21
	1949	0	2	12	8	6
Average	1948	60	101	85	83	74
	1949	25	60	41	55	41
Rotifera						
Maximum	1948	5,409	4,098	1,310	515	285
	1949	2,642	2,963	766	694	599
Minimum	1948	12	39	94	51	31
	1949	7	3	9	0	0
Average	1948	1,242	1,231	489	231	128
	1949	1,034	601	187	173	146
Protozoa						
Maximum	1948	825	825	1,300	1,719	1,193
	1949	1,380	1,460	3,620	2,660	1,120
Minimum	1948	0	0	0	0	0
	1949	3	0	0	0	0
Average	1948	255	242	405	603	222
	1949	311	436	641	381	170
Average Total Zooplankton Exclusive of Protozoa	1948	1,619	1,566	671	386	250
	1949	1,121	738	333	310	200

Highest populations of Cladocera were attained in the spring, reaching a maximum of 642 per liter in 1948 and 176 per liter in 1949. Cladoceran populations in 1948 were greatest at Stations 1 and 2 and decreased down the lake to Station 5. In 1949, however, the populations at Stations 1

and 2 decreased tremendously in size from 1948, whereas, the populations at Station 3, 4, and 5 were not significantly different from 1948 populations at these stations. *Bosmina longirostris* was by far the most abundant species.

Two large pulses of Rotifera made up largely of Polyarthra were produced, one in late spring and another in late summer. In 1948, the highest average population was 2,124 per liter in the spring and 779 in late summer. The spring pulse of 1949 averaged 1,511 per liter and the late summer maximum was 1,142. During both years, rotifers were most abundant at Station 1 and 2 and declined at each successive station down the lake, becoming a minimum at Station 5. In 1949, there was a significant decline in rotifer populations at Stations 1, 2, and 3, whereas populations at Stations 4 and 5 were not significantly different from 1948 populations.

It is apparent from an examination of Table IX that the highest zooplankton populations were present at Stations 1 and 2. The average populations were lower at all stations in 1949, and the greatest decline in population occurred at Stations 1 and 2. There was no significant difference in phytoplankton levels to account for this uneven horizontal distribution of zooplankton. Neither was there any decrease in phytoplankton production in 1949 as compared with 1948 to account for the drop in zooplankton populations between the two years. It is significant that the highest zooplankton populations were present at Stations 1 and 2, both of which are located in the area of the lake which was first submerged by the rise in water level in 1947. The high populations occurring here are correlated with the large amounts of vegetation which was submerged by the rise of water level.

Similar observations have been made on other reservoirs. Thompson (1946) in his study of Lady Bower Reservoir found that planktonic Entomostraca and Rotatoria occurred in abundance throughout most of the year, despite the relative paucity of the flora (caused probably by the large-scale replacement of the water by inflow and outflow). He concluded that the abundance of these animals was chiefly caused by the decay of submerged grass, and that planktonic algae did not form a large part of their food. The submerged organic matter probably entered the trophic cycle of the lake in the form of cell substance of heterotrophic bacteria involved in decomposition which were in turn utilized by the zooplankton. If one were to assume that the organic matter submerged by the water was the cause of the higher zooplankton production in the upper end of the lake, a logical deduction would be that, with the passage of time, zooplankton populations would decrease in the upper end of the lake and populations in the lower end would decrease to a lesser extent as the decaying material was consumed.

Bottom Fauna

Bottom fauna samples were taken during October-November, 1947 and in May, 1948 at various depths. The 1947 collections of 72 samples yielded 361 Chaoborus and 23 chironomid larvae. Expressed in numbers per square meter, the population of Chaoborus amounted to 189 and chironomids 11, or a total of 200 per square meter. The 1948 collections consisted of 63 samples which yielded 64 Chaoborus and 65 chironomid larvae, amounting to 15 Chaoborus and 16 chironomids per square meter, or a total of 31 per square meter. The paucity of bottom fauna in Atwood Lake compared to other lakes was very striking and was probably correlated with the low production of phytoplankton in the lake. Deevey and Bishop (1942) from an analysis of data from 33 lakes, found a relatively high correlation between plankton (measured by chlorophyll content of the water) and bottom fauna.

Gross Productivity

During the period April 8 to July 11, 1949, a series of determinations of oxygen production and oxygen consumption at the surface, two, four, six, and eight meter levels was made using the black-and-white bottle technique. Gross photosynthesis was greatest in the 0-2 meter stratum (Average 0.51 ppm. O_2/48 hr.), slightly less in the 2-4 meter layer (Average 0.48 ppm. O_2/48 hr.) and decreased to 0.33 ppm. O_2/48 hr. at the 4-6 meter depth and 0.26 ppm. O_2/48 hr. at the 6-8 meter level. The relatively high average rate of gross photosynthesis observed in the 6-8 meter level was largely due to a high rate of photosynthesis, 1.49 ppm. O_2/48 hr., which occurred at this depth on June 30. This event coincided with a period of very calm weather at which the maximum Secchi disc reading of 2.5 meters occurred and resulted in a rise of oxygen concentration of 1.11 ppm. in the 6-8 meter level between June 30 and July 11. The average gross rate of photosynthesis for all water levels was 0.39 ppm. O_2/48 hr.

Gross oxygen consumption was at a maximum in the 2-4 meter level (0.61 ppm. O_2/48 hr.) compared to the average oxygen consumption in the 0-2 meter stratum of 0.51 ppm. O_2/48 hr. and in the 4-6 meter layer of 0.50 ppm. O_2/48 hr. Oxygen consumption in the 6-8 meter level 0.54 ppm. O_2/48 hr.) was greater than any stratum except

the 2-4 meter level. This was probably due to the close proximity of this layer to the lake bottom and the effect of the oxygen consumption of decaying organic matter in the bottom soils.

Only in the 0-2 meter layer did the average gross rate of oxygen production equal the average gross rate of oxygen consumption. The average rate of oxygen consumption exceeded the average rate of oxygen production by increasing amounts with an increase in depth. Consequently, the average amount of oxygen released by photosynthesis at all depths (0.39 ppm. O_2/48 hr.) was only 73% of the oxygen consumed by respiration (0.54 ppm. O_2/48 hr.).

In order to determine how closely the net rate of oxygen consumption, *i.e.* gross oxygen consumption minus gross oxygen production, compared with the actual rate at which oxygen was consumed in the lake, the average rate of oxygen decline below the four meter level was calculated from the data on oxygen concentrations between April 8 and July 11. This layer of water was selected since it would be less affected by turbulence and consequent oxygen exchange with atmosphere. The average rate of oxygen decline in the 4-8 meter stratum from April 8 to July 11 was 0.13 ppm. O_2/day compared to the calculated rate from oxygen production and consumption data of 0.12 ppm. O_2/day. Hence, for this portion of the lake, at least, the black and white bottle method gave a measure of oxygen relations that was in close agreement with the actual observed oxygen consumption.

On a surface-area basis, the average rate of gross photosynthesis was 906 mg. $O_2/m.^2$/day which is equivalent to 850 mg. glucose/$m.^2$/day. The maximum observed rate was 1,851 mg. glucose/$m.^2$/day and the minimum was 210 mg. glucose/$m.^2$/day. In terms of energy utilization, the average glucose production of 850 mg. glucose/$m.^2$/day is equivalent to a fixation of 0.318 gm. cal./$cm.^2$/day. The average daily amount of solar radiation received at the surface at Washington, D. C., which is approximately the same latitude as Atwood Lake, amounted to 504 gm. cal./$cm.^2$/day during the period of study. The efficiency of gross production in Atwood amounted to 0.063% during the period of study compared to an efficiency of 0.40% in Lake Mendota (Juday 1940), an extremely productive lake.

During this period, phytoplankton populations in Atwood Lake ranged from 2,447 to 240,030 cells or colonies per liter and averaged 48,458 cells or colonies per liter. No correlation was found between phytoplankton populations and rates of photosynthesis.

Discussion

The fish population following drainage consisted mainly of black and white crappie in poor condition, stunted bluegill, such rough fish as carp, gizzard shad, and a small population of largemouth bass which was the only game fish that grew at a satisfactory rate. Black and white crappies and bluegills grew at a satisfactory rate the first year following drainage and at a very low rate the second year.

There is evidence that under some conditions the biotic activities of carp can have an unfavorable effect on game fish populations. Ricker and Gottschalk (1940) attributed the gradual increase of turbidity, the disappearance of vegetation, and the decline of game fish in Bass Lake, Indiana to an overabundance of carp. Large numbers of rough fish were removed by seining in 1935 and 1936. In 1936, the water cleared, vegetation increased in extent and density, and the number of game fish increased rapidly. Up to 1940, there had been no significant reversion to conditions existing prior to 1935.

Bennett (1943) stated that rough fish greatly influence the success of more desirable fish in artificial lakes. A change in the game fish population may come about through disturbance during the spawning period of the nest building fishes, or rough fish (through greatly increased turbidity) may cause such a modification of the environment that it becomes unsuitable to the game and pan fish.

The presence of carp in Atwood following drainage certainly had no effect on the spawning success of any of the game fish, because large numbers of crappies, bluegills, and largemouth bass were spawned in 1947. No evidence was found that carp were instrumental in making the lake turbid in the years 1947-1949. The only time turbidity values were high was during periods of heavy runoff. Iron-humus colloidal complexes were responsible for poor light penetration in the shallower upper end of the lake. Rooted aquatics spread into suitable shallow areas during this period. Extensive weed beds will not be present in the upper end of the lake unless a decrease in color production results in better light penetration.

The percentage of carp caught in test nets steadily decreased from the time of impoundment in 1940 until the lake was drained. The same thing happened again after the lake was re-impounded in 1947. Hence, any unfavorable effect the carp were having would decrease as the size of the population decreased.

On the basis of these facts, the author can see little justification for the assumption that carp

were making Atwood Lake unsuitable for game fish. It would seem that there is something more fundamental associated with the large and stunted fish populations than mere competition by carp. The limnology of Atwood throws considerable light on this problem.

In the final analysis the productivity of any body of water depends upon the efficiency with which plants convert radiant energy into potential energy of organic material which becomes available to the fish, directly or indirectly through various food chains.

Plants living in water can be divided into two groups, rooted aquatics and phytoplankton. During this study, rooted aquatics did not contribute much to the biological economy of Atwood because of their limited extent. Standing crops of phytoplankton and bottom fauna were extremely small.

When the water level was raised in 1947, a large quantity of organic matter entered the trophic cycle. As a result, standing crops of zooplankton were high during the summer of 1948 in the portion of the lake flooded for the first time. The standing crop of zooplankton decreased in this area in 1949 and can be expected to decrease further as a result of the continued decay of the original organic matter.

The elimination of a portion of the fish population by drainage and the raising of the water level created conditions favorable to the production of a dominant year class of fish spawned in the spring of 1947. The large amount of zooplankton furnished ample food for young of the year fish and the elimination of most of the larger carnivorous fish in the drainage process permitted survival of these fish.

The fish grew rapidly the first year. With a dwindling food supply after consumption of the initial organic matter and the inability of the lake to produce sufficient fish food (especially bottom fauna), growth rates of the dominant species of game fish declined rapidly the second year. The only species of game fish that grew fast enough to maintain good fishing was the largemouth bass. Since there was an abundant supply of undersized fish upon which the bass could feed, this growth is not surprising. However, there is some question as to the ability of the bass to maintain itself in high numbers in the future. As a result of the predation pressure of the enormous crappie population in the lake, certainly the rates of bass recruitment will be lower than in 1947 when hundreds of young bass could be seen along the shore. It has been experienced elsewhere (Bennett 1943) that small bass populations are frequently associated with large crappie populations and *vice versa*.

Summary

A two-year study was made of the physical, chemical, and biological characteristics of Atwood Lake, a flood control reservoir in eastern Ohio with special reference to the effect of these factors on the production of desirable crops of game fish. Previously, the lake was drained to get rid of rough fish thought to be creating conditions unfavorable for game and pan fish.

Poor light penetration in the upper end of the lake was due largely to the presence of iron-humus colloids. Turbidity was important only during the spring months as a result of surface runoff.

Phytoplankton crops were extremely low in comparison to more productive lakes. Phytoplankton numbers were greater in 1949 than in 1948, and marked variations in horizontal distribution were noted during both years.

Zooplankton populations were greater in the upper end of the lake where a large amount of vegetation was inundated by the rise in water level of the lake in 1947. Zooplankton crops were smaller in 1949 compared to 1948; the greatest decline occurred in the upper end of the lake.

Bottom fauna consisted of Chaoborus and chironomid larvae. Compared to other lakes, bottom fauna was very low, which was correlated with low phytoplankton production.

The average rate of gross photosynthesis was 906 mg. $0_2/m.^2/day$, and the average rate of oxygen consumption amounted to 1,262 mg. $0_2/m.^2/day$. The efficiency of gross production in Atwood Lake was 0.063 per cent.

The fish population consisted mainly of black and white crappie in very poor condition, stunted bluegill, such rough fish as carp, gizzard shad, and a small population of largemouth bass. The bass was the only game fish that grew at a satisfactory rate. Black and white crappies and bluegills grew at satisfactory rates the first year following drainage and at very low rates the second year. The satisfactory growth rates of these fish in the first year were correlated with high zooplankton populations resulting from the submergence of vegetation when the lake level was raised following drainage. Declining zooplankton and a paucity of bottom fauna were suggested as the cause of the slower growth rates subsequent to the first year. The satisfactory growth rate of largemouth bass was attributed to the abundance of undersized fish upon which the bass could prey.

No evidence was obtained to show that carp were affecting the productivity of the lake either by making the water turbid, eliminating weed beds, or by interference with spawning activities of game fish.

It was concluded that the natural level of productivity of Atwood Lake was too low to maintain satisfactory growth rates of the populations of game fish produced following drainage.

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AN ANALYSIS OF THE SPRUCE-FIR COMMUNITY ON THE KAIBAB PLATEAU, ARIZONA

JOHN MERKLE[1]

Department of Biology, Agricultural and Mechanical College of Texas, College Station, Texas

Introduction

During the summer of 1951, sociological data were obtained in the spruce-fir forest on the Kaibab Plateau of northern Arizona. The area of study includes the highest elevations in Arizona north of the Grand Canyon of the Colorado River. The study was limited to the area inside Grand Canyon National Park because of its virgin condition. The area in the Kaibab National Forest to the north is utilized for grazing by livestock.

The past work on the spruce-fir forest has recently been extensively treated by Oosting and Reed (1952) in connection with the analysis of this type of community in the Medicine Bow Mountains of Wyoming. They also present an extensive bibliography.

[1] The nomenclature of the plants follows that of Kearney and Peebles (1951). The author wishes to express appreciation to several people for aid in the work: Mr. Louis Schellbach, Park Naturalist, for interest and encouragement in several ways, and Mr. E. T. Christensen, Assistant Park Naturalist in charge on the North Rim, for extra time in my work schedule as seasonal Ranger-Naturalist to pursue the field research. Dr. T. H. Kearney identified the more difficult plants, and Dr. J. T. Howell identified the species of *Carex*. My wife, Cherrie Merkle helped gather data in the field and later in compilation of data and typing. Specimens of all plants listed are deposited in the Herbarium of Grand Canyon National Park.

Geology and Soils

The Kaibab Plateau is the highest of several in the Grand Canyon section with an altitude ranging from 7500-9200 feet. The southern part of this and adjacent plateaus bordering Grand Canyon on the north side are commonly known as the North Rim. The plateau is capped by the Kaibab limestone, which is maturely dissected by rounded valleys of gentle slope not more than 300 or 400 feet deep. These valleys are streamless despite the ample rains in summer and snows in winter (often over 10 feet) due to seepage into the highly porous limestone. Some springs are found and there are small sinks with ponds of fresh water (Fenneman 1931). The rock is composed chiefly of gray, crystalline and cherty limestone, but includes some beds of calcareous sandstone. Also there are local redbeds of crumbly fine sand and silt (McKee 1938). The soils are derived from the Kaibab limestone and are included in one of the areas of Helmer-Santa-Benewah series of gray-brown podzolic soils (Ableiter, *et al.* 1938).

Climate

The climate of the Kaibab Plateau is cool and moist, especially at highest elevations. Weather records are kept at the Bright Angel Ranger Station, North Rim Headquarters of the Park, at

8400 feet elevation (Greening 1941). These records show an average January temperature of 21°F., a July average of 61.6°, with a maximum of 91° and a minimum of —25° through 1938. The average date of the last killing frost in spring is June 14, the first in the fall is September 15, giving an average growing season of 93 days. The average annual precipitation is about 27 inches occurring in two seasons, the maximum during July, August, and September, usually as heavy local afternoon showers. Most of the remainder occurs from December to March as snow, with seasonal amounts of more than 10 feet frequently recorded. The area studied is about 10 miles north and at a higher elevation. The growing season is shorter, temperatures are lower, precipitation is slightly higher, but no records are available for exact amounts. The area is included in the "humid, microthermal, rainfall adequate at all seasons" climatic province described by Thornthwaite (1931).

Vegetation

The spruces and firs in Arizona occupy the coldest, wettest, and highest forested areas on the Mogollon Mesa, White Mountains, San Francisco Mountains, and on the Kaibab Plateau at elevations of 8200-12,000 feet (Nichol 1937, Little 1950). The general vegetation of the Plateau has been described and mapped by Rasmussen (1941). *Picea engelmanni* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), *A. concolor* (white fir), and *Populus tremuloides* (aspen) are the most important trees on the ridge tops, north- and northeast-facing slopes above 8700 feet (Fig. 1). *Pseudotsuga taxifolia* (Douglas fir) and *Pinus ponderosa* (ponderosa pine) occur chiefly as larger trees. The south and west slopes are covered predominantly with white fir, ponderosa pine, and aspen. *Picea pungens* (blue spruce) occurs chiefly at the lower edges of the spruce-fir zone. *Pinus aristata* (foxtail pine) does not occur here, but is found in southern Utah and the San Francisco Mountains to the south.

Rasmussen (1941) gives the altitudinal ranges of the spruce-fir as 8200-9200 feet. Actually, below 8700 feet the spruces and subalpine fir are generally limited to steep northerly and easterly slopes and some narrow valleys. Other slopes, ridge tops, and flat or rolling areas at 8250-8700 feet are covered by an extensive ponderosa pine-white fir community with no spruce or subalpine fir. Rasmussen's map of the spruce-fir includes both communities. Below 8250 feet is an extensive ponderosa pine consociation, and below 7300-7500 feet is the pinyon-juniper community.

There is very little shrubby and herbaceous cover in the spruce-fir forest (Fig. 1). Only two shrubs, *Juniperus communis* (prostrate juniper) and *Berberis repens* (creeping mahonia) are present. The most important herbs are *Poa fendleriana* (mutton grass), *Bromus ciliatus* (fringed brome), *Carex siccata, Erigeron formosissimus* (daisy), *Fragaria ovalis* (strawberry), and *Senecio uintahensis* (groundsel). All are found chiefly in openings in the woods.

Methods

The vegetation was analyzed by the quadrat method. Curves constructed from the data indicated that the ½ sq. m. size (½ x 1) was the most efficient size to sample the herbaceous plants according to the "break of the curve" (Braun-Blanquet 1932, Cain 1938, and others). With this size 68 per cent of all the herbaceous species seen in the community were sampled with 50 quadrats spaced at 50 meter intervals along compass lines through the woods. The shrubs were sampled with 1 x 2 meter quadrats. At the same time 10 x 10 meter quadrats were used to obtain data for the trees including density, frequency, height classes, basal area (1 inch or more d.b.h.), and cover. These are presented in Table II and as phytographs modified from Lutz (1930). Curves constructed to indicate the minimum number of quadrats showed that the "break of the curve" for 5 per cent increase in species to 10 percent increase in area (Cain 1938, Oosting 1948) occurred at about the 15th quadrat. Fifty per cent of the herbaceous species, the most important in the community, were sampled with the first 15 quadrats. The data in Table I are given for the 50 quadrats. Because of the scarcity and scattered distribution of the understory plants, larger quadrats or a greater number of small quadrats take very little longer if one should feel the need for more complete sampling.

Discussion

The tabulated data include a total of 45 vascular species with 7 trees, 2 shrubs, and 24 herbs sampled. One other shrub and 11 herbs were seen but not sampled. The 5 tree species with the highest frequencies are the most important (Table II). Aspen and Engelmann spruce are the most widespread on all sites. Aspen is often in large stands with spruces and firs reproducing underneath. The occurrence of aspen in such large numbers is explained by fires in the past century, and before, which burned unchecked, except for probable local suppression by stockmen who were active on the plateau from 1885. In recent years, fires have been effectively suppressed by the Forest Service and the National

FIG. 1. View on ridge top in spruce-fir forest with aspen (white bark), spruce, fir, and ponderosa pine. Note small foliage spread in spruce and firs. Foreground: rocky soil, prostrate juniper lower right, young aspen killed by deer browsing, young spruce.

Park Service. "There is a general belief among local foresters that the Kaibab Forest suffered a terrific fire [at] some indefinite time in the last two centuries" (correspondence, Supervisor, Kaibab National Forest). Since a high percentage of the summer thunderstorms start fires by lightning, the plateau has undoubtedly had numerous fires every year for centuries. The topography does not seem the type to support a large holocaustic fire as on more mountainous terrain, but many small fires can be quite destructive. There are blackened stumps and logs scattered throughout

TABLE I. *Sociological data for the Picea-Abies community with per cent of frequency (F), cover (C), and life-form (LF) for each species based on 50 ½ x 1 m. quadrats for herbs and 50 1 x 2 m. plots for shrubs*

Species	F	C	LF
Shrubs			
Juniperus communis	22	2.0	Ph
Berberis repens	8	0	Ch
Amelanchier sp.*	..	0	Ch
Herbs			
Poa fendleriana	32	1.3	H
Bromus ciliatus	16	0.3	H
Pedicularis centranthera	12	0.1	H
Carex spp.	12	0.1	G
Erigeron formosissimus	10	0.1	H
Senecio unitahensis	8	0	H
Hieracium fendleri	8	0	H
Fragaria ovalis	6	0	H
Goldyera oblongifolia	4	0	H
Antennaria aprica	4	0	H
Sitanion hystrix	4	0	H
Arenaria fendleri	4	0	H
Silene scouleri	4	0	H
Erigeron ursinus	2	0	H
Antennaria marginata	2	0	H
Geranium richardsonii	2	0	H
Castilleja confusa	2	0	H
Agrostis scabra	2	0	H
Aster adscendens	2	0	H
Pseudocymopterus montanus	2	0	H
Pteridium aquilinum	2	0	G
Epilobium angustifolium	2	0	H
Polygonum sawatchense	2	0	Th
*Pyrola virens**	..	0	H
*Pyrola picta**	..	0	H
*Blepharoneuron trichlepis**	..	0	H
*Chimaphila umbellata**	..	0	H
*Corallorhiza maculata**	..	0	G
*Ramischia secunda**	..	0	H
*Draba asprella**	..	0	Th
*Pterospora andromedea**	..	0	G
*Gayophytum nuttallii**	..	0	Th
*Aquilegia coerulea**	..	0	H
*Ranunculus flammula**	..	0	H

Carex spp.—*C. siccata* and *C. occidentalis*.
0—less than 0.1 percent cover.
*—present, but not in samples.

the woods that are the result of fires before the services were in the area.

Aspen invades burned areas rapidly and is gradually replaced by spruces and firs that germinate and grow among the aspens, finally overtopping them. This process is probably slower on the Kaibab Plateau than farther north or at higher altitudes, because the invading trees are less thick and aspens are able to thrive for a long time among the climax trees (Fig. 1). The greatest number of aspens occur in the smallest height class (Table II) usually as root sprouts in more open areas. In the more closed areas, this species is represented chiefly by large trees. The low number in height class 2 can be attributed to heavy summer browsing by a large deer herd. Large numbers of stems are in class 2, but severe browsing has killed the tops and new buds have sprouted below the 2 foot level. Most of these sprouts are also browsed during the summer. The death of these small aspens in great numbers is due principally to browsing and not shade, because they are in openings and have teeth marks on the twigs. The low number of representatives in class 3 can be attributed to the "devastation of the entire young aspen growth" by the large deer population of the 1920's and 1930's (Rasmussen 1941). There are some local stands of small trees 8-15 feet tall that have started growth since the drastic reduction of the herd. Now these trees show a definite "browse line" 4-5 feet above the ground. In all stands on the plateau, there is a conspicuous lack of trees between these small sizes and the large size; trees which should have started during the 1920's and early 1930's. The maximum size sampled was 17 inches d.b.h., with most larger trees 6-12 inches d.b.h. Maximum height was approximately 80 feet, generally 60-70. The dead specimens of large aspen were found chiefly in more dense woods.

The two species characteristic of subalpine forests, Engelmann spruce and subalpine fir, have relatively high frequency, density, and basal area. Subalpine fir is more patchwise, with fewer numbers on ridge tops, southerly and westerly slopes, and greater numbers on northerly and easterly slopes. It has higher cover than the other conifers. The largest tree was 16 inches d.b.h. Some layering was noted. Spruce is more evenly distributed, has slightly higher basal area because of greater diameters in the larger height class. The maximum size sampled was 25 inches d.b.h., but a stump was found that measured 37 inches. Maximum height for all coniferous trees is within a range of 90-110 feet.

The presence of white fir, Douglas fir, and ponderosa pine is a result of the relatively low elevation, which is within the tolerance limits of these species. However, all are more abundant below 8700 feet, where they form a distinct community down to 8250 feet. White fir appears to be invading the spruce-fir rather successfully as it outnumbers Engelmann spruce in total numbers and in the smaller height classes. The maximum size of white fir seen in this community was 22 inches d.b.h., but trees of more than 30 inches were seen in the community below.

Individual trees of the first four species listed in Table II usually have low cover value. The crown area of the larger trees often covers only 4-10 sq. m. of ground area. Foliage of large aspens is limited to the top (Fig. 1).

The high basal area of Douglas fir is due to the preponderance of large trees, the maximum being 30 inches d.b.h. with several over 16 inches. The

TABLE II. *Data used in construction of phytographs for the trees of the spruce-fir community*

Species	Frequency %	Numbers in each height class*						Basal area		Cover %
		1	2	3	4	Total	% of total	Sq. ft.	Per cent	
Populus tremuloides	100	621 (96)	30 (18)	2 (2)	102 (23)	755 (139)	43 (75)	41 (6)	17	9
Picea engelmanni	90	60	57 (2)	30 (4)	54 (6)	201 (12)	12 (6)	44 (4)	18	9
Abies lasiocarpa	80	162	100 (3)	63 (7)	90 (12)	415 (22)	23 (12)	40 (5)	17	13
Abies concolor	74	110	86	46	30 (8)	272 (8)	16 (4)	26 (3)	11	6
Pseudotsuga taxifolia	64	9	8	11 (2)	39 (2)	67 (4)	3 (2)	50 (58)†	21	8
Pinus ponderosa	32	7	3	1	18 (1)	29 (1)	2 (0.5)	33 (78)†	14	3
Picea pungens	18	1	5	1	5 (1)	12 (1)	1 (0.5)	6 (113)†	3	1
Total						1751 (187)		240	..	49

*1, 0-2 ft.; 2, 2-10 ft.; 3, 10-25 ft.; 4, over 25 ft. tall. ()Dead trees standing. †square inches.

maximum size of ponderosa pine was 33 inches, one was 31 inches, and 9 were over 16 inches d.b.h. These two species are being replaced since their reproduction rate is low. The phytographs (Fig. 2) compare all the trees graphically.

Oosting and Reed (1952) diagram the cover formed by the trees of the spruce-fir community on the Medicine Bow Mountains, Wyoming as class 5 of Braun-Blanquet (1932), which would indicate more than 75 per cent compared to a

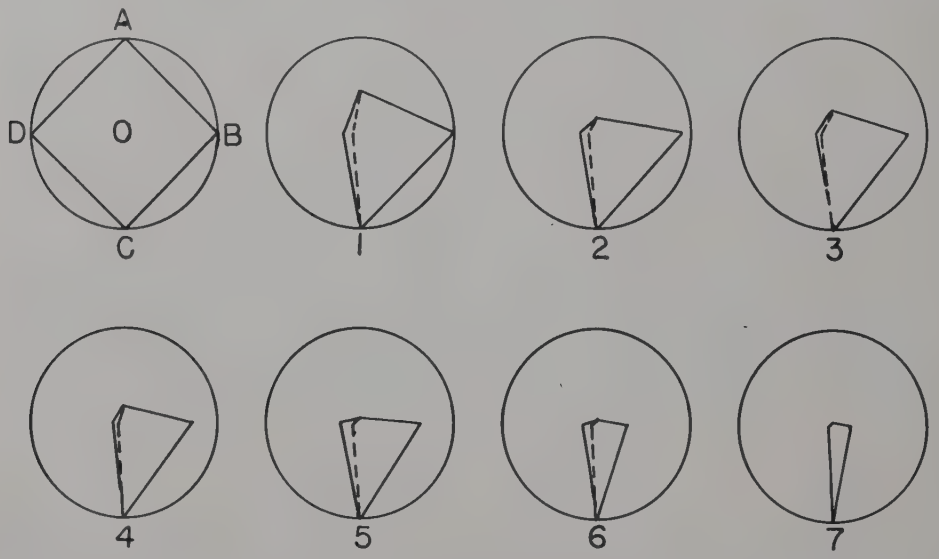

FIG. 2. Phytographs of trees based on data in Table II. Upper left is standard with radii OA—per cent of total abundance, OB—per cent of frequency, OC—number of height classes, OD—per cent of basal area. The dash line is obtained with OD as per cent of ground covered. 1—*Populus tremuloides*, 2—*Picea engelmanni*, 3—*Abies lasiocarpa*, 4—*Abies concolor*, 5—*Pseudotsuga taxifolia*, 6—*Pinus ponderosa*, and 7—*Picea pungens*.

total of only 49 per cent tree cover for the Kaibab Plateau. They list only Engelmann spruce, subalpine fir, and lodgepole pine (*Pinus contorta* Dougl.). Their study area was above the elevation limit of white fir, Douglas fir, and ponderosa pine, while the high cover prevents the survival of aspen. Lodgepole pine does not occur in Arizona. Comparing densities of Engelmann spruce and subalpine fir shows that considerably greater numbers of each occur in a given unit area on the Medicine Bow Mountains than on the Kaibab Plateau.

A few ring counts were obtained from stumps and logs of trees removed from roads. The average number per inch for spruce and subalpine fir was 9-16, and total number per tree was 78-164, this larger number on the 37 inch spruce stump. There was no evidence that the trees had been suppressed for long periods. Some of the small trees under the large ones, and in thick stands show suppressed growth at present. A 30 inch pine had 287 rings, a 30 inch Douglas fir had 375 rings, a 12 inch white fir had 138 rings, and a 10 inch aspen had 69 rings.

The shrub and herb understory contains only a few relatively important species (Table I) all of which are rather widely scattered. *Juniperus communis* is limited to the spruce-fir areas including the slopes and valleys occupied by these trees below 8700 feet. *Berberis repens* extends down into the ponderosa pine forest below 8250 feet. *Amelanchier* is apparently an accidental here, probably from seeds brought in by birds. Three small plants were found together, each less than a foot high and semi-prostrate. It seems improbable that they will ever fruit or even survive for long. This genus is represented by several species at lower elevations, especially on slopes of ravines and along the canyon rim where it extends down several hundred feet with other brush genera to form a chaparral.

Only 5 herbaceous genera provide at least 0.1 per cent cover each. *Poa, Pedicularis,* and *Ranunculus* fruit in June, and the remainder mature in July, August, and early September. *Pyrola virens, P. picta, Ramischia, Aquilegia, Epilobium,* and *Chimaphila* are characteristic of the spruce-fir and are very rare or absent below 8700 feet. The others are much more abundant in the nearby meadows and lower forest while *Poa, Sitanion, Hieracium, Carex* (both species), *Draba, Silene,* and *Antennaria* (both species) are common in the ponderosa pine forest below 8250 feet.

There is a total of 45 vascular species in the spruce-fir of the Kaibab Plateau compared to 46 in the Medicine Bow Mountains, 97 in the Sierra Nevada (Oosting and Billings 1943), 59 in the Appalachian Mountains (Oosting and Billings 1951), and 36 in west-central Colorado (McCullough 1948).

The life-forms of all the species were determined in accordance with the system of Raunkiaer (1934). The five general life-form classes were utilized and are: phanerophytes (Ph), chamaephytes (Ch), hemicryptophytes (H), geophytes (G), and therophytes (Th). The distribution of the species in these classes (Raunkiaer normal in parentheses) is 21 (46) per cent, 2.5 (9) per cent, 62 (26) per cent, 7 (6) per cent, and 7 (13) per cent respectively. This distribution indicates a hemicryptophytic climate.

The distribution in frequency classes of all species sampled, with Raunkiaer normal in parentheses (Ooosting 1948), is as follows: class 1—75 (53) per cent, 2—10 (14) per cent, 3—0 (9) per cent, 4—10 (8) per cent, and 5—7 (16) per cent. The high number of species in this community in class 1 (species with 1—20 per cent frequency) indicates a highly heterogeneous distribution.

Summary

During the summer of 1951, sociological data were obtained for the spruce-fir forest on the Kaibab Plateau in Grand Canyon National Park, Arizona. The study was made within the elevation range of 8700 to 9200 feet, which is the maximum on the plateau.

The spruce-fir here can hardly be referred entirely to the *Picea-Abies* association as defined by various authors. In addition to *Picea engelmanni* (Engelmann spruce) and *Abies lasiocarpa* (subalpine fir), trees of the montane forest below are relatively abundant. These include *Pinus ponderosa* (ponderosa pine), *Abies concolor* (white fir), and *Pseudotsuga taxifolia* (Douglas fir). The great abundance of *Populus tremuloides* (aspen) is attributed to extensive fires of the past two centuries and the low cover value of the other trees. *Picea pungens* (blue spruce) occurs at the lower edge of the forest and is not very abundant, although below 8700 feet it may be in the bottom of small valleys and along the edges of some meadows.

Only two shrubs, *Juniperus communis* (prostrate juniper) and *Berberis repens* (creeping mahonia) are characteristic of the community, but the latter is more abundant at lower elevations. The most important herbs are *Poa fendleriana* (mutton grass), *Bromus ciliatus* (fringed brome), *Carex siccata, Erigeron formosissimus* (daisy), *Fragaria ovalis* (strawberry), and *Senecio uintahensis* (groundsel). All have low abundance, frequency, and cover.

The community was analyzed with 50 sets of quadrats, ½ sq.m. for herbs, 2 sq.m. for shrubs, and 100 sq.m. for trees. Tables present frequency, cover, and life-form for shrubs and herbs, and frequency, density, height classes, basal area, and cover for trees. The total cover for trees is 49 per cent and for shrubs and herbs about 5 per cent. The effect of the large deer population, both past and present, on aspen is discussed.

A total of 45 species was found, including 7 trees, 3 shrubs, and 35 herbs.

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FACTORS CONTROLLING THE DISTRIBUTION OF OYSTERS IN A NEUTRAL ESTUARY[1]

Nelson Marshall

Oceanographic Institute, Florida State University, Tallahassee

In analyzing factors influencing the natural distribution of oysters, *Crassostrea virginica,* we are often faced with so many variables that the role of each is not clear. By contrast Alligator Harbor, the area discussed herein, is a very simple, neutral estuary rather uniform as to many factors and thus more readily understood in terms of the variables that do exist.

The various studies undertaken on Alligator Harbor by the Oceanographic Institute of Florida State University have been tapped for information pertinent to this discussion of oyster distribution. Mr. Charles S. Yentsch has been especially helpful in examining certain sampling strips for the presence of oyster spat. Dr. F. C. W. Olson has been very helpful in the comprehension of our hydrographic observations. Dr. H. J. Humm has aided in many ways in his capacity as Director of the Institute.

[1] Contribution No. 18, Oceanographic Institute, Florida State University.

Alligator Harbor (Fig. 1), is located along the northern Gulf Coast of Florida (lat. 29° 55′ N, long. 84° 25′ W). A shallow bar which emerges on low tides crosses the mouth and, since there are no cuts or channels except around the ends of this bar, the Harbor's waters are somewhat distinct in terms of circulation, land drainage effects, biological populations, etc. Essentially rectangular in outline, Alligator Harbor is about 4½ miles long and about 1¼ miles wide. The bottom contours are gradual and, with the exception of one deeper hole and the channels at the bay mouth, do not exceed eight feet at mean low water.

The distribution of oyster bars in Alligator Harbor is shown in Figure 1. They occur only above mean low water on moderately firm elevated areas of mixed sand and mud. They do not occur on the more mature sandy shorelines but are common on the marsh fronts. There is a discontinuity or a pattern of breaks between individual bars

FIG. 1. Alligator Harbor, showing distribution of oyster bars, coring sites and Stations 318, 313, 308 and H.

though the intervening areas often have, as best I have been able to observe, the same characteristics as the adjacent substrata on which the oysters are growing.

Basic to an analysis of oyster distribution is the consideration of the hydrography of the area, especially as it bears on the dispersal of the planktonic oyster larvae. Accordingly, the following observed features of Alligator Harbor are presented:

(1) The only drainage tributaries are the meandering channels in the bordering salt marshes and these carry little fresh water. A series of consecutive observations was made on two such tributary channels from 23:60 on April 24 to 06:30 on April 25, 1953. The changes in the smaller of the two were slight. The larger, studied at a station (Station H on Fig. 1) about a mile by straight line from harbor waters, yielded salinities from 24.8 parts per thousand on the high tide to 7.5 parts per thousand on the low. Simultaneous observations at Station 308 at the head of the harbor yielded salinities ranging only from 29.6 to 30.3 parts per thousand.

(2) Other drainage must come under the little-understood category of seepage. Some such seepage may take place through the harbor bottom. It has been observed along the shoreline February 27, 1952 when a sample of the waters draining from the intertidal zone was collected and was found to have a salinity of 6.3 parts per thousand whereas the salinity in the Harbor at that time measured 27.4 parts per thousand.

(3) Changes in salinity in the harbor, more or less seasonal (Fig. 2), seem to be caused primarily by changes in the Gulf waters outside and these are affected by larger tributaries of the region. Such changes affect the harbor waters in a comparatively uniform manner (Table I and Fig. 3). The slight gradients that do exist along the 4½ mile axis of the estuary may be inverse with the higher salinities toward the head, direct with the higher salinities nearer the Gulf, or mixed. This suggests that drainage and rainfall on the one hand and evaporation and transpiration on the other tend to counterbalance, approximating the theoretical neutral estuary mentioned by Pritchard (1952).

(4) In this shallow estuary, having but slight surface salinity gradients and being affected by the mixing action of tidal and wind currents, vertical stratification is very weak (Figures 3 and 4).

(5) The mean tidal range is 1.92 feet and the extremes, backed by wind effects, frequently exceed 5 feet. Though all tides are semidiurnal they are frequently so skewed at the maximum declination of the moon as to approximate the diurnal pattern. Winds seem to have a simple direct effect on tides that is readily observed when the wind velocity exceeds 20 m.p.h. The pushing of water before a driving wind is characteristically followed by a seiche with a period of about two hours quite distinct though interwoven into the tidal pattern. These comments on tides and seiches are derived chiefly from a water level recorder operated at the laboratory site since December, 1950. Analyses of the records have been made by Dr. F. C. W. Olson (unpublished).

(6) Currents are chiefly of tidal origin with wind as the major modifying factor. Though directions are varied by the wind and physiography of the basin, the gross pattern involves alternate up-harbor easterly flood currents and down-harbor westerly ebb currents. One series of observations, the twelve-hour cycle studied on April 11, 1953, gives the basic pattern since the tides of the day were of the unskewed semi-diurnal type and were little affected by winds. On this date the maximum flood current near the mouth (Station 318, Fig. 1) was 0.5 knots; the maximum ebb was 0.4 knots. The maximum flood at mid-harbor (Station 313) was 0.2 knots; the maximum ebb was 0.5 knots. The maximum ebb and the maximum flood near the head of the harbor (Station 308) were 0.1 knots.

(7) The harbor is highly turbid except when

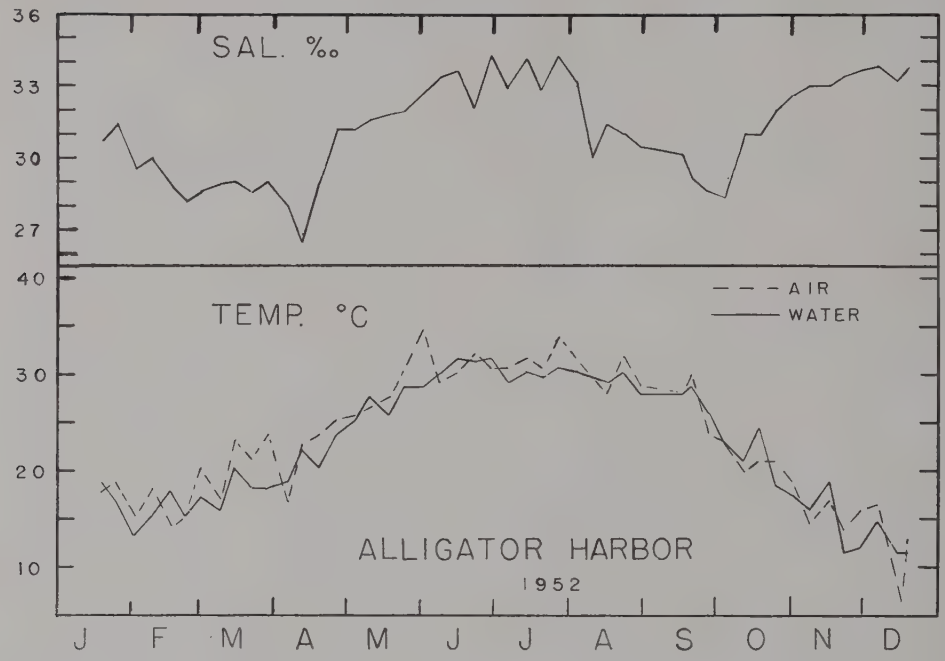

FIG. 2. Mid-day salinities and temperatures at the marine laboratory pier, Alligator Harbor. Data provided by George D. Grice, Jr.

TABLE I. *Surface salinities (0/00) near the mouth, at mid-harbor, and near the head of Alligator Harbor. Number of readings is given in parentheses when entry is an average of more than one*

Date	Near mouth Station 318	Mid-harbor Station 313	Near head Station 308
April 5, 1952	27.1(6)*	28.4(4)	27.9(4)†
April 26, 1952	31.4**	31.4	30.3
May 17, 1952	33.6(3)††	33.0(2)††	32.3
July 30, 1952	33.5(2)††	34.1(3)††	36.0
Oct. 9, 1952	30.8	30.3	29.5
Oct. 15, 1952	31.4	30.6	30.2
Oct. 25, 1952	32.3	31.8	31.5
Nov. 30, 1952	33.6*	33.4	33.5
Feb. 14, 1953	31.4(3)	31.5(3)	31.1(3)
Feb. 27, 1953	28.9(3)	29.3(3)	30.0(3)
March 8, 1953	30.1(3)	30.5(3)	30.0(3)
March 20, 1953	30.6(3)	30.6(3)	29.8(3)
April 11, 1953	30.0(37)	29.3(38)	29.0(38)

*Alligator Pt. Channel, 500 yards south of Station 318.
†Station 309, 500 yards west of Station 308.
**Station 218, 500 yards north of Station 318.
††Average from neighboring stations.

prolonged calms permit settling. This turbidity is very irregular, varying in place and time, and is generally greatest when the waters are warm. The cause is not understood.

(8) Consecutive salinity and temperature observations taken at frequent intervals from fixed stations, such as those presented in Figures 3 and 4, suggest the existence of numerous minor water masses within the harbor. Undoubtedly these continuously change and vanish through mixing; however their transient existence interrupts to some extent the rather homogeneous character of the water.

This review indicates that hydrographic gradients, barriers and other water conditions that might limit the dispersal of planktonic organisms about Alligator Harbor are at a minimum. On the contrary, and as might be surmised on theoretical grounds for a neutral estuary, these hydrographic features should disperse planktonic forms in a widespread manner.

Pertinent data relative to this is available from a grid of masonite sampling strips, 1⅝ inches wide and extending from the surface to the bottom, that were set up as invertebrate collectors at 500-yard intervals about the harbor (1000-yard intervals toward the mouth). One series of strips was exposed at these stations from March 23 to April 29, 1953, a second series from May 4 to June 10, and a third series of fewer strips from August 5 to September 1, thereby covering some of the more intense setting periods for sessile invertebrates.

Such general invertebrate collectors are not comparable to shell bags and other specialized collectors set out specifically for oyster spat counts;

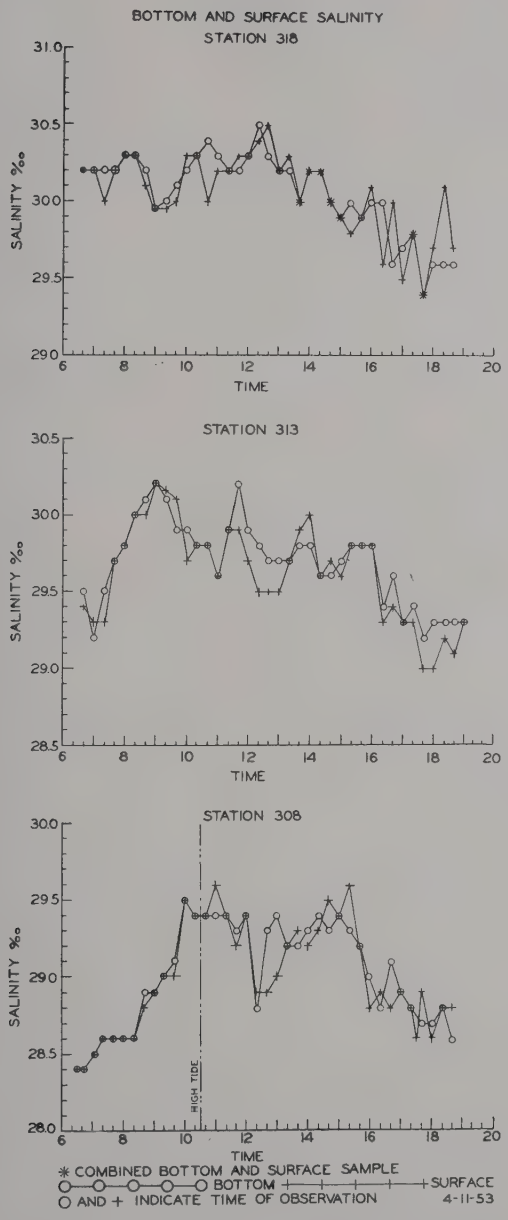

FIG. 3. Surface and bottom salinities at the mouth (Station 318), at mid-harbor (Station 313), and at the headwaters (Station 308) in Alligator Harbor during tidal cycle April 11, 1953.

furthermore, with the high predation extant in the harbor as discussed below, one would not expect a four- to five-week exposure to yield spat representative of the original set. Even so the strips exposed often showed large numbers of small oysters occurring at varied depths. Where

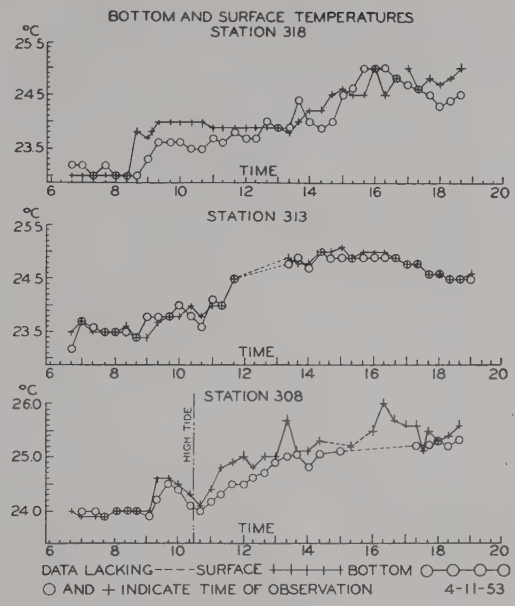

FIG. 4. Surface and bottom temperatures at the mouth (Station 318), at mid-harbor (Station 313), and at the headwaters (Station 308) in Alligator Harbor during tidal cycle April 11, 1953.

noted they were restricted to the smooth reverse side of the masonite adjacent to the supporting stake. This side may have been relatively free of the common predators. Also, on this reverse side were many patches so close to the stake that barnacles, bryozoans and other more upright growths did not develop, thus leaving comparative blanks where oysters could be found.

The slabs exposed March 23 to April 29 were without spat. Of the 47 slabs exposed May 3 to June 10, spat were noted on all but 8, five of which were in very shallow water along the north shore and 3 of these 5 were within 300 yards of oyster bars. The largest count noted was that of 480 spat from ¼ to ⅜ inches in size on an eight foot strip about three miles from the nearest oyster bar.

Actually it was not until May, the time of the second exposures, that water temperatures rose above 25° C. (Fig. 4), the minimum required to bring about mass spawning according to the findings of Ingle (1951) in the nearby Apalachicola Bay region. Temperatures continued high through the third exposure, August 5-September 1, but there were few oysters on the fourteen slabs set out and collected. The few oysters that were noted, however, represented setting in every major portion of the harbor, even on the slab along the north shore near the mouth, over 4 miles from the nearest oyster bar in the estuary.

Also supporting the concept of widespread dispersal are the counts made by Yentsch (1953) of the development of the barnacles, bryozoans and hydrozoans that predominated on the slabs that were exposed from March 23 to April 29. His data on the common estuarine barnacle, *Balanus eburneus,* for which the masonite slab provides an excellent setting surface, showed the widespread plankton dispersal quite vividly inasmuch as this species was abundant on all of the 44 slabs exposed.

Assuming an unlimited larval dispersal and spatfall, the actual limited distribution of the natural oyster bars must be a function of later survival and development. Again hydrographic conditions are important and basic. The above emphasis on the lack of barriers and the general circulation and mixing in such an estuary does not imply uniform hydrographic conditions equally favorable for development at all locations; however, with the mixing that occurs its seems improbable that any properties of the water such as dissolved chemicals, nutrients and planktonic food would be a major limiting factor causing the highly restricted oyster-bar distribution in this estuary.

Though they may have been common but unnoticed in the crevices of the predominating growths, the lack of oysters noted on portions of the masonite slabs that supported growths of barnacles, bryozoans, hydrozoans and other more or less upright animals may suggest biological competition as limiting oyster distribution. Undoubtedly this was significant during these short exposure periods; however, in a setting favorable to oysters the latter will commonly displace or at least live in association with such other sessile invertebrates. In the less saline waters typical of Tampa Bay, for example, I have found oysters common both above and below the low-tide line, often dominating and with barnacles, bryozoans etc., growing secondarily on their shells.

The fact that oysters are known in many areas to survive and thrive best when completely submerged focuses attention on the notable lack of survival below mean low water in Alligator Harbor. This suggests that the abundant predators in the estuary, including the gastropods, *Thais floridana, Busycon perversum, Melongena corona, Urosalpynx tampaensis,* and the crabs, *Callinectes sapidus* and *Menippe mercenaria,* cause this limitation in vertical range. To check this, a hundred single oysters were placed below mean low water adjacent to one of the oyster bars. On each side of this plat were placed two cages each containing a hundred oysters. These were set out August 26, 1952 and removed for examination November 5, 1952 at which time there were 9 live oysters in the unprotected patch compared to 86 and 84 in the cages. Some unprotected natural clumps of oysters had been removed from the bar to be observed on the test area below mean low water during this period. Mortalities were also high on these unprotected oysters but such clumped material does not provide specific mortality records as given above.

The role of predation, coupled with a consideration of physiographic features, provides an explanation of the actal distribution of oysters in the estuary. The oyster must have a substratum sufficiently firm for the development of oyster bars and free of shifting, smothering sands. Predation has limited oyster bars to sites where such substrata extend above mean low water, such elevation being essential to oyster survival in this area. Cores made through three representative oyster bars in the harbor (for coring locations see Fig. 1) yielded shell fragments only to depths approximately in line with mean low water. This indicates that the same controlling forces have been in operation throughout the history of the bars.

These explanations of distribution do not account for the discontinuity or breaks in the bars, for the passes have substrata that may have all the above-mentioned favorable environmental features. Except to suggest, as others have in verbal discussions, that this is simply a mechanical effect of the ebbing and flooding of waters, I can offer no explanation.

Experienced oyster biologists repeatedly warn that ecological relationships are far more complex than the above account would suggest and they can cite localities where the pattern described herein does not apply. Admittedly this is a simplification but it reveals basic controlling forces which operate in this relatively simple body of water and which, with due qualifications, may be quite applicable elsewhere. It is common knowledge that many areas of continuing high salinities support oysters at intertidal levels only, although, as shown by McNulty (1953), the set may be very intense at lower levels. Comparative salinity tolerances have not been established; nevertheless many of the larger gastropod predators of the type known in Alligator Harbor are obviously restricted to higher salinities and are not as euryhaline as the oyster.

Summary and Conclusions

In an unstratified neutral estuary such as Alligator Harbor, oyster larvae are dispersed over the entire area. The distribution of oyster bars, which is quite restricted on the the other hand, is controlled by an interplay of physiographic and

biological factors. In Alligator Harbor oyster bar development occurs where the substratum is firm, free of shifting sands and elevated to the intertidal level, partially out of range of intense depredation by carnivorous gastropods and other common oyster predators.

Hydrographic conditions in a neutral estuary tend to effect a widespread dispersal of the plankton and the planktonic larvae. In such estuaries restricted distributions must be accounted for by more extrinsic physical features of the environment, by biological activity, or by minor deviations from the prevailing neutral conditions.

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EVIDENCE OF FOUR PINE SPECIES FROM FOSSIL POLLEN IN MICHIGAN[1]

John F. Grayson

Department of Botany, University of Michigan, Ann Arbor, Michigan

One of the vexing problems of palynology is that of species identification. Although generic determination is not usually difficult, very few pollen grains can be identified to species by morphological details. This is obviously a serious handicap in palynological studies since, within a genus, the various species often play different ecological roles. The significance of a genus in a pollen profile may depend upon the particular species present except where genera are composed of species of similar ecological status. In the present state of palynology, only general trends can be considered significant since the profiles are largely based on generic composition.

In the absence of morphological details permitting the identification of species of a genus, the size-frequency method sometimes provides clues to, or even highly probable determinations of, fossil species. In the cases where species can be indicated, information about the succession of vegetation and climate based on fossil evidence is revealed in much more detail and becomes, therefore, more significant.

Early size-frequency studies were made in Europe by Stark (1927, 1929), Hörmann (1929), and Bertsch (1931), all of whom worked on pine or birch pollen. Such investigations were not pursued very vigorously because of the prevalent feeling that the results were not conclusive. In America, Cain (1940) initiated the first studies of size-frequency characteristics of pollen grains by examining 12 species of pine that are found in eastern United States. This study was undertaken in an effort to identify the fossil pines in the spectra of buried organic soils in the Piedmont near Spartanburg, South Carolina (Cain 1944). The size-frequency curve for fossil pine grains was trimodal. The size of grains represented by these modes compared rather well with the size-frequency curves of pollen of modern *Pinus banksiana*,[2] *P. glabra*, and *P. rigida*. The circumstantial evidence for the former existence of *Pinus banksiana* in a region several hundred miles south of its present boundary was especially strong because it proved to have the smallest pollen of all the eastern species and was closely coincident with the smallest of the three modes for fossil grains.

This initial study was based on a single collection of pollen for each species. Subsequently, the question of variation was explored. In one paper Cain and Cain (1944) reported on 11 collections of *Pinus palustris* distributed from Texas to North Carolina. In this species, they found little variation among the samples as to size characteristics, but in another study dealing with *Pinus echinata* (Cain and Cain 1948a) they found a wide variation. Furthermore there apparently exists a geographic cline for this species, for the collections from the northwestern part of the range had grains consistently and significantly larger than from the southern range.

In another size-frequency study, Cain (1948) demonstrated the probability that *Picea rubens*

[1] The author wishes to express his sincere gratitude to Stanley A. Cain for his guidance and encouragement throughout the course of this project.

[2] The nomenclature of tree species follows that of Little (1953).

grew in southeastern Michigan in early post-glacial time. The ecological possibilities of the method were suggested by two other studies from southeastern Michigan. Cain and Cain (1948b), in the Sodon Lake studies, found a trimodal size-frequency curve for pine of the Boreal period which could be referred to *Pinus banksiana, P. resinosa,* and *P. strobus.* These results were duplicated by Cain, Cain, and Thomson (1951) for Heart Lake. In both cases, the size-frequency curves for successive samples indicated that *Pinus banksiana* was initially the most important species of the group and that *P. strobus* tended to increase in percentage composition as the pine period waned. Such results coincide with expectations based on their present ecology and distributions.

Besides these eastern studies, Hansen (1947) has made good use of the size-frequency technique in a series of studies in the Pacific Northwest, dealing mostly with conifers. Hansen's studies, spread as they are over a wide geographic area, have revealed much about succession and the ranges of species that would have remained unknown on a basis of simple generic determinations.

Methods

The material for the present study comes from slides prepared and analyzed by Cain and Andersen in an unpublished pollen investigation of sediments from George Reserve, Livingston County, Michigan, about 25 miles northwest of Ann Arbor. The sediments were obtained from the bottom of a small pond that is a relict of a former glacial lake. Sampling extended from the six-foot level below the shallow water surface to a maximum depth of 57 feet. The sediments are essentially an unstratified gyttja except that the lower 10.5 feet contain progressively more clay or rock flour. The lower spectra, from 57 up to 45 feet, were dominated by spruce. This period was followed by a pine period. Pine was first found at 45 feet, and the percentage of pine in the spectra increased rapidly to a maximum of 73 per cent of all arboreal pollen at the 41-foot level. At the 36-foot level, where spruce disappeared, pine was reduced to 19 per cent. From 37 feet upward, oak was predominant genus. Slides prepared from samples taken at foot-level intervals from 43 to 36 feet, inclusively, were studied. Above 36 feet, the pine grains were scarce and one additional set of measurements was developed from the 36-27 foot levels. Because of peculiarities of the results, to be discussed later, slides were prepared of material from the 38.5-foot level (See Fig. 1).

At each foot-level, 100 pine grains were measured without any selection except for whole, inflated grains with suitable orientation. The dimension used for these measurements was the internal grain breadth between the wing insertions at the base of the dorsal cap. Any grain lying with its diameter parallel with the slide could be measured whether seen in dorsal, ventral, or polar view. Measurements were made with a binocular microscope, using a 43X objective and 10X oculars. The unit of measurement was an eyepiece micrometer line equal to 1.17 microns. In general, the samples were prepared with KOH followed by the Erdtman acetolysis treatment. In a few cases, it was also necessary to treat the samples with hydrofluoric acid.

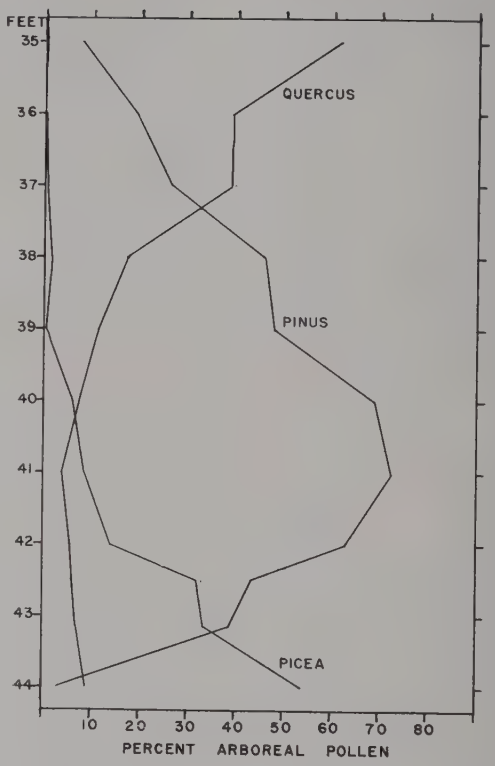

Fig. 1. Section of pollen profile showing the trends of the three major foot levels.

Results

Table I shows the size-frequency distribution of 1000 fossil *Pinus* pollen grains. The length of these grains ranged from 30 to 63 ocular lines or from 35 to 74 microns. A study of these data reveals that the 5 lower levels of the pine period, between 39 and 43 feet, show only minor variations. Figure 2 shows the combined results of

these levels. Three modes, designated as "A," "B," and "C" are obvious at 37, 41, and 45 ocular lines or 43, 48, and 53 microns. At the 38.5 foot level, mode "A" has disappeared and a new mode appears at 51 ocular lines or 60 microns (designated as "D"). From the 27 to the 38 foot levels, there is no sign of modes "A" or "B." Only modes "C" and "D" are present. Between the 27 and the 38 foot levels, however, mode "C" becomes progressively smaller as mode "D" becomes progressively larger.

TABLE I. *Size-frequency distribution of fossil pollen grains*

Size		No. of grains in sediments (foot levels)										
Lines*	Microns	27-35'	36'	37'	38'	38½'	39'	40'	41'	42'	43'	Total 27-43'
31	36.3	..	..	..	..	..	..	..	..	..	1	1
32	37.4	..	..	..	..	..	1	..	..	1	1	3
33	38.6	..	..	..	..	..	3	..	..	1	2	6
34	39.8	..	..	..	..	1	4	2	1	2	1	11
35	40.9	..	..	..	2	3	4	2	1	5	2	19
36	42.1	..	..	..	1	2	6	3	2	6	7	27
37	43.3	..	..	2	1	3	10	1	8	11	7	43
38	44.5	..	1	1	2	3	5	4	5	8	9	38
39	45.6	..	1	2	2	4	3	6	5	3	3	29
40	46.8	1	2	3	4	9	10	7	9	9	11	65
41	48.0	2	3	3	3	11	14	18	10	12	10	86
42	49.1	2	2	3	2	7	6	11	5	7	8	53
43	50.3	3	1	4	2	3	3	6	3	5	4	34
44	51.5	6	4	5	7	7	7	9	9	6	7	67
45	53.8	8	8	13	15	15	10	14	20	11	13	127
46	55.0	4	4	6	8	6	6	7	6	6	5	58
47	56.2	3	3	5	5	4	2	2	5	3	4	36
48	57.3	3	5	5	5	3	2	2	3	2	3	33
49	58.5	2	3	4	4	3	1	3	3	2	1	26
50	59.7	8	7	6	5	5	2	3	4	..	1	41
51	60.8	17	15	14	9	7	1	..	1	..	..	64
52	62.0	6	10	7	4	3	..	..	..	..	..	30
53	63.2	3	4	3	5	1	..	..	..	..	..	16
54	64.3	5	4	4	4	..	..	..	..	..	..	17
55	65.5	4	6	3	3	..	..	..	..	..	..	16
56	66.7	3	4	2	3	..	..	..	..	..	..	12
57	67.9	3	3	2	2	..	..	..	..	..	..	10
58	69.0	4	3	2	2	..	..	..	..	..	..	11
59	70.2	3	3	1	..	..	..	..	..	..	..	7
60	71.3	4	3	..	..	..	..	..	..	..	..	7
61	72.4	3	1	..	..	..	..	..	..	..	..	4
62	73.7	2	..	..	..	..	..	..	..	..	..	2
63	74.9	1	..	..	..	..	..	..	..	..	..	1
Total		100	100	100	100	100	100	100	100	100	100	1000

*1 line = 1.17 microns.

From these data it is obvious that there are four distinct peaks found in this size-frequency analysis which seem to indicate four species of pine.

DISCUSSION

The above size-frequency data suggest that four species of pine have contributed to the pollen rain during the sedimentation of the George Reserve pond. During the spruce period and until the decline of the pine period, three species of pine (indicated by modes "A," "B," and "C") were present in this area. At the 38.5 foot level, a change in the vegetation pattern seems to have occurred. Although no major break is evident in the pollen profile (See Fig. 1), the smallest mode ("A") has disappeared and a new, larger mode ("D" appears, indicating that one species of pine has been replaced by another species. From the 38 foot level upward, the species of pine represented by mode "B" has also disappeared and modes "C" and "D" persist. A study of the foot levels between 27 and 38 feet shows mode "C" becoming smaller as mode "D" becomes correspondingly larger, thus indicating an increase of the species represented by mode "D" and a decrease of the species representd by mode "C."

At the present time, only *Pinus strobus* (white pine) is native to this area although *Pinus banksiana* (jack pine) and *Pinus resinosa* (red pine) are found within approximately 100 miles. Cain and Cain (1948b) and Cain, Cain, and Thomson (1951) in their size-frequency studies of fossil pine pollen in two different bogs in Oakland County, Michigan, found good evidence for three species of pine. By comparison with size-frequency characteristics of modern pollen of *Pinus banksiana, P. resinosa,* and *P. strobus,* they showed good correlation between the size-frequency curves of the fossil and modern pollen. Their interpretation was that *Pinus banksiana* and *P. resinosa* were present during the latter part of the spruce maximum and were the dominant species during the pine maximum. Their trimodal curve became evident at the decline of the pine maximum and this was interpreted as the appearance of *Pinus strobus.*

Essentially the same trends have been found in this work as were found by the authors cited above. The difference appears to be that a fourth species appeared later in this area in addition to the usual three.

Since Cain, Cain, and Thomson (1951) have shown the probability of *Pinus banksiana, P. resinosa,* and *P. strobus* having been present in Michigan during the pine maximum and since modes "A," "B," and "C" of this work correlate well with the means of modern pollen of these three species (see Table II), it seems likely that the modes "A," "B," and "C" in this study represent *Pinus banksiana, P. resinosa,* and *P. strobus* respectively. Mode "D" would then represent a species of pine that is no longer present in Michigan.

In attempting to establish the identity of the fourth species of pine discovered in this work, size-frequency studies were made on a number of species of western and southern pines. Table II

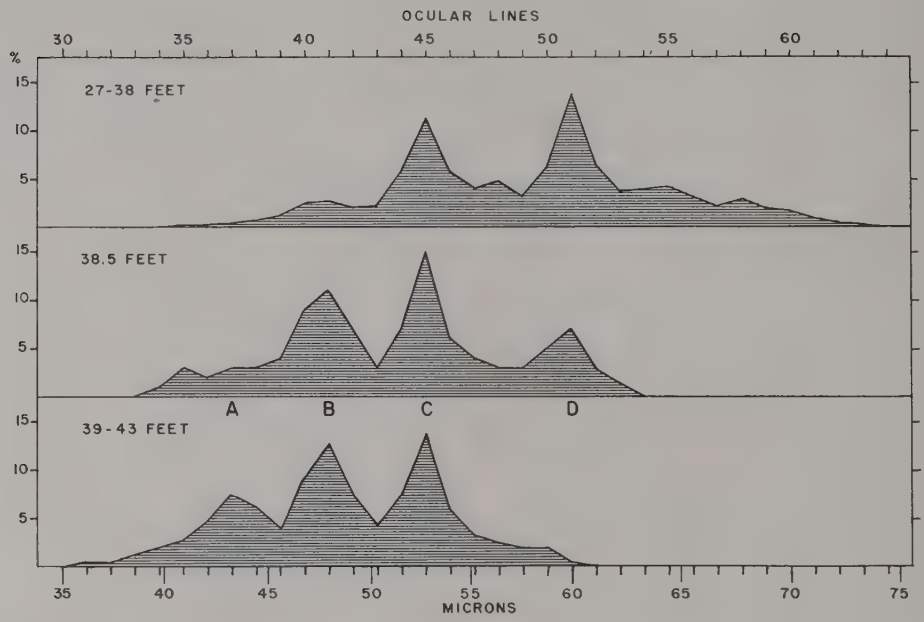

FIG. 2. Composite size-frequency curves of *Pinus* pollens. The nature of these curves indicate the presence of four species of *Pinus* pollens and the succession of these species.

TABLE II. *Size-frequency characteristics of modern pine pollen (measurements in microns)*

Species of *Pinus*	Number	Range	Mean	Standard deviation
P. banksiana (a)	1850	33.7-55.1	44.79	1.92
P. resinosa (a)	1500	38.2-56.6	46.00	2.85
P. strobus (a)	1250	39.8-62.7	50.38	4.03
P. albicaulis (b)	100	46.8-62.0	53.12	2.85
P. contcrta (c)	100	42.2-56.2	48.50	2.75
P. flexilis (d)	100	46-8.59.7	53.75	2.66
P. monticola (e)	100	48.0-70.4	59.20	4.42
P. virginiana (f)	100	35.1-56.1	45.85	4.42
P. virginiana (g)	100	37.4-51.5	44.60	3.04
P. rigida (h)	100	44.5-59.7	52.15	3.28

Data for (a) were taken from Cain and Cain (1948b). Samples b-f were secured from herbarium material of the National Herbarium, Washington, D. C., by A. C. Smith and were collected at: (b) Spanish Basin, Montana, (c) Victoria, British Columbia, (d) Baldy, New Mexico, (e) Washington, (f) Appomattox, Virginia. Samples g-h were secured from herbarium material of the West Virginia University Herbarium by E. A. Bartholomew and were collected at: Okonoko, Hampshire Co., West Virginia.

shows the results of these studies as well as some statistics on *Pinus banksiana, P. resinosa,* and *P. strobus* as found by Cain and Cain (1948b.) From Table II it can be observed that none of the species of pine, except *Pinus monticola,* have a mean near that of mode "D" which is at 61 microns. *Pinus monticola* does have approximately the same mean as mode "D." The probability of mode "D" representing *Pinus monticola* seems quite remote because the present range of *Pinus monticola* is far-western, extending from British Columbia to California. The present range of *Pinus ponderosa* which extends as far east as South Dakota and Nebraska suggests the possibility of a further eastern range of this species in the post-Pleistocene. Hansen (1947) indicates that the size of modern *Pinus ponderosa* is large. However, not enough statistical data are available for any conclusion at this time and the need for intensive study of other American species than those already published is strongly indicated.

With regard to the southern and eastern species of pine, the ranges and ecologic requirements of three suggest the possibility of a further northern or western range in the past. They are *Pinus rigida, P. virginiana,* and *P. echinata.* From Table II it can be seen that the size of the pollen grains of *Pinus rigida* and *P. virginiana* seem to be too small to account for mode "D." *Pinus echinata,* however, was found by Cain and Cain (1948a) to have a geographic cline with the northern collections consistently larger than the southern. The means of these collections reached as high as 60 microns, which is where mode "D" of this work is located. The present range of *Pinus echinata* extends as far north as southern Illinois, Ohio, Pennsylvania, and New York. It is usually found on dry and sandy soils.

Since mode "D" appears at the end of the pine maximum and the beginning of the oak maximum, the climate at this time was undoubtedly changing

from a cool, moist to a warmer and drier climate. Mode "D" could well represent the furthermost northern limit of one of the southern pines, such as *Pinus echinata*. As the climate became still warmer and drier, the range of this species appears to have receded southward, after only a brief excursion northward.

The evidence that is offered in this study is circumstantial and the statistical basis for modern pollen is inadequate. However, this evidence does reveal a story that is compatible with the known principles of ecology and biogeography. A serious problem that must be faced in this type of work is the lack of sufficient data on the size-frequency characteristics of modern pollen. Because herbaria characteristically contain very little if any pollen-bearing specimens of conifers, it is difficult to extend such studies. Cain has already attacked this problem in a number of ways and is continuing to do so. Upon completion of his Pollen Atlas, which is now being written, a tremendous volume of size-frequency data for modern pollen will be available, not only for *Pinus* but for many of the other genera. Another problem in this type of work is the effect of fossilization and methods of preparation on the size of the pollen grains. At the present time, insufficient work has been done on this problem to make correction factors possible.

From this size-frequency study, and those conducted by other workers in the field, there can be little doubt concerning the validity of the method for fossil materials. The various polymodal curves that result from size-frequency analysis, and the consistency of these curves as to the micron size of the various modes throughout the sediments suggest that statistically different populations have contributed to the pollen rain, and that the populations represent different species of pine.

Summary

A size-frequency study was made of the fossil pollen found in the sediments of a pond in Livingston County, Michigan. A well defined, trimodal size-frequency curve was found to exist between the levels of 39 and 43 feet. This trimodal curve is believed to represent *Pinus banksiana, P. resinosa,* and *P. strobus*. All three of these species of pine are found in this area at the present time. At the 38.5 foot level, another trimodal curve appears. This differs from the former in that the smallest mode has disappeared and a larger mode has appeared while the other modes do not shift their positions. This trimodal curve is taken to represent the disappearance of *Pinus banksiana* from the area and the appearance of a a fourth species of pine as yet unidentified, but possibly *Pinus echinata*. From the 38 foot level upward, a constant bimodal curve is formed. The mode presumed to be *Pinus resinosa* has disappeared.

Modern pollen from several western and southern species of pine was analysed for size-frequency characteristics. All of the western species were found to be too small to account for the large mode except *Pinus monticola*. The present range of *Pinus monticola* indicates the improbability of this species being present in Michigan at the close of the pine period. *Pinus ponderosa* is suggested as a possible western species, but the lack of adequate size-frequency data prevents any further speculation. Of the southern species, *Pinus rigida* and *Pinus virginiana* are rejected as possibilities because of the small size of their pollen grains. *Pinus echinata* seems to be the most plausible explanation for the large mode. The pollen size and the present range of *Pinus echinata* strongly suggest a northern extension of its range in the past, but further size-frequency analysis of contemporary pollen of these species will be necessary before an interpretation of Michigan species "D" can be made with assurance.

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QUANTITATIVE STUDIES OF PROTOZOAN POPULATIONS FROM TWO AREAS OF PYMATUNING LAKE, PENNSYLVANIA[1]

HOWARD D. ORR
Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania

Pymatuning Lake is a large artificial lake on the Pennsylvania-Ohio boundary, resulting from a dam built on the Shenago River at Jamestown, Pennsylvania, in 1933. Its uppermost section, Sanctuary Lake, covers 2000 acres, has a mean depth of five feet and a maximum depth of nine feet. This section is of interest not only because of its high plankton productivity (Tryon and Jackson 1952), but because the northern portion of it receives raw sewage from the town of Linesville by way of Linesville Creek. The southern portion, which is somewhat larger, drains a five-mile swamp. Mixing of the two types of drainage is prevented by an area of emergent vegetation except in the lowermost part of the lake (see Fig. 1). Thus an opportunity exists to study the effects of the organic pollution by comparing life in these two portions. The present study, conducted during the summer of 1951, was an attempt to compare the populations of Protozoa.

FIG. 1. Map of Sanctuary Lake portion of Pymatuning Lake showing the two collecting areas and the six sampling stations.

[1] Contribution No. 9, Pymatuning Laboratory of Field Biology.

METHODS

Three open-water stations were selected for each drainage area. Three samples were taken at each station once each week over a seven-week period from July 6 to August 22. Collections were made by submerging quart jars below the surface of the water. Samples were concentrated to 215 ml. by the method proposed by Hall (1924). One 32-ml. portion of each of these quantities was concentrated to 3 ml. by means of a hand centrifuge. Counts of the protozoa in these samples were made by examining them drop by drop, following the general method suggested by Lackey (1942).

Temperatures were recorded for each station, and the pH of each sample was determined by means of a Beckman meter. Oxygen, carbon dioxide and carbonate determinations were made by standard methods.

RESULTS

Water temperatures ranged from 69° to 85°F. (20.6 to 29.4°C.) in Sanctuary Lake during the eight weeks. For the sewage area the range of pH was 7.8 to 9.5 as compared to 7.5 to 8.9 in the swamp area. The ranges of dissolved oxygen in parts per million for the sewage and swamp were 6.4 to 12.6 and 6.0 to 10.4 respectively. Sewage drainage ranged from 4.0 ppm. carbon dioxide to 18.0 ppm. carbonates. Swamp drainage varied from 6.0 ppm. carbon dioxide to 6.0 ppm. carbonates.

Protozoa samples showed some difference between areas when viewed qualitatively. Four ciliates were found in samples from the sewage area (one of these, *Epistylis* sp., was observed only once) which were not taken in the swamp area. One chlorophyll-bearing flagellate, *Phacus pleuronectes*, was far more common in the swamp area than in the sewage area. *Actinophrys sol* appeared in one sample taken from the sewage area. In general, however, the species composition of the two areas was similar. Table I shows the species found and gives the number of samples for each area in which they were observed.

So far as numbers of individuals are concerned, six species constituted the great majority of the populations. Table II shows the average weekly count for each of these from each area over the seven-week period. Two species, *Pandorina*

morum and *Trachelomonas hispida,* seemed to show seasonal population growth and decline. These are represented graphically in Figure 2.

TABLE I. *Species of protozoa collected in Sanctuary Lake with the numbers of samples from each area in which they occurred*

	Sewage	Swamp
Chilomonas paramecium	3	2
Cryptomonas ovata	6	2
Phacus pleuronectes	2	10
Euglena spirogyra	13	10
Volvox globatcr	3	2
Ceratium hirundinella	10	17
Trachelomonas hispida	21	21
Eudorina elegans	4	3
Glenodinium sp.	2	2
Pandcrina morum	15	20
Actinophrys sol	1	0
Difflugia oblonga	4	10
Halteria grandinella	20	18
Coleps hirtus	7	15
Stokesia vernalis	4	0
Codonella cratera	5	3
Paradileptus conicus	5	0
Vorticella campanula	3	0
Epistylis sp.	1	0

TABLE II. *Average weekly counts of the numbers per 251 ml. of several species of protozoa collected from two areas of Pymatuning Lake from July 6 to August 22, 1951*

Week	Area	Coleps	Pandorina	Euglena	Trache-lomonas	Ceratium	Halteria
1	Sewage	0.2	0	0	0	2.6	0.8
	Swamp	0.3	0	0	0	1.3	0.4
2	Sewage	0.1	3.2	3.2	5.4	0.1	0.1
	Swamp	0	1.1	0.4	2.3	1.0	1.5
3	Sewage	0.2	1.6	0.2	10.2	0	1.6
	Swamp	2.7	1.5	0.7	4.8	0.2	1.3
4	Sewage	0.2	0	2.4	24.3	0	0.3
	Swamp	0.8	5.1	0.8	6.6	0.2	1.3
5	Sewage	0.2	0	1.5	17.7	0.1	0.8
	Swamp	0.3	6.4	0.3	14.7	1.6	1.4
6	Sewage	0	0.6	0.3	32.0	0.2	1.4
	Swamp	0.3	3.3	0.8	15.1	1.0	1.2
7	Sewage	0	1.3	0.7	29.2	0.3	0.5
	Swamp	0	0.5	0.1	9.2	1.0	0.5
8	Sewage	0	0.3	0	15.2	0.3	1.4
	Swamp	0.2	1.0	0	5.2	1.1	0.8

The remaining four species showed only weekly variation.

A standard analysis of variance was used to determine the significance of the data (symbols follow Snedecor, 1946). *F*-values exceeding the 1% level were obtained in analyzing the samples taken from the two areas for all of the six species except *Halteria grandinella.* Thus it is assumed that the samples were not drawn from a common population.

DISCUSSION

It is difficult to explain the differences between the populations of Protozoa in the two areas. Of

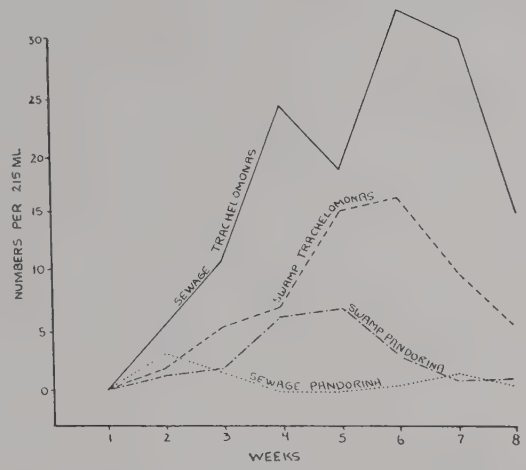

FIG. 2. Graph showing the counts for *Trachelomonas hispida* and *Pandorina morum* in two distinct areas of Pymatuning Lake over the period July 6 to August 22, 1951.

the six predominant species, only two were higher in numbers of individuals in the sewage area, while three were more abundant in the swamp area. This information, plus the fact that *Halteria* populations showed no significant difference between the areas reflects the complexity of the situation. The environmental factors measured do not seem to offer an explanation because their ranges are not beyond the optima of the species. If pollution is effective, it is probably an indirect factor. In most cases of pollution the number of species decreases, while the numbers of individuals increase (Lackey 1938). In Sanctuary Lake more species were observed in the area subjected to pollution. It is possible that raw sewage may increase food in the form of bacteria and thus favor holozoic types. Qualitative sampling in Linesville Creek revealed that better than 80% of the species were ciliates.

Evidence of the complete mixing of the waters of both areas was observed. *Difflugia oblonga* tests would not ordinarily be found near the surface. Samples collected at various depths were quite similar to samples collected at the surface. Attempts to collect bottom samples were unsuccessful because of the constant turbulent condition of the bottom.

Any attempt to compare the protozoan populations of Sanctuary Lake with those of other situations must be qualitative, because previous workers have paid little attention to the quantitative aspects of this group. From the qualitative standpoint Sanctuary Lake differs in the percentage composition by taxonomic classes. Edmondson (1920) gives the typical percentages for lakes

as follows: Mastigophora 14%, Sarcodina 19%, and Ciliata 67%. In Sanctuary Lake more than 50% of the species were Mastigophora. Even sampling at various stations around the edge of the lake revealed a similar picture. Either the locality is unique as a lake, or it might better be classified as a large pond.

More information on protozoan populations in their natural environments is needed before limnological situations can be completely understood. Such knowledge would also be of use to the worker who is interested in laboratory study of the dynamics of protozoan populations. However, a less time-consuming method of sampling must be developed first.

Summary

1. Sanctuary Lake, the upper portion of Pymatuning Lake, Pennsylvania, is subjected to two types of drainage: swamp and sewage.

2. Samples from both drainage areas were collected eight times at weekly intervals during July and August, 1951.

3. Protozoan counts showed a quantitative and qualitative difference between the populations of the two areas.

4. Differences were not due to any of the environmental factors measured. Neither area was more productive for all species. Pollution probably exerts an indirect influence by increasing available food in the form of bacteria.

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ECOLOGY OF THE OPUNTIAE IN THE BIG BEND REGION OF TEXAS[1]

Margery Anthony
Department of Biology, Chico State College, Chico, California

Introduction

One of the richest but least known of our southwestern cactus areas lies in Trans-Pecos Texas, where the Rio Grande, in a giant curve, delimits a large portion of basin and range country known as the Big Bend Region. With great topographic diversity offering habitats for a wide variety of forms, this area makes an excellent meeting ground for faunal and floral forms of four adjacent biotic provinces.

Taxonomic analysis of natural populations of Opuntiae, recognizing 31 species, hybrids and varieties (Table I), necessarily accompanied these observations of ecological relationships but will be published elsewhere.

[1] The author expresses sincere appreciation to Professor Harley H. Bartlett, Director of the Botanical Gardens, and to Dr. Elzada U. Clover, Department of Botany, for their encouragement and assistance during this research, which is in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Michigan. Field work was made possible by a Research Assistantship at the Botanical Gardens.

Thanks are also extended to Barton H. Warnock, Chairman, Department of Biology, Sul Ross State Teachers College, Alpine, Texas, and to officials of the Big Bend National Park, for their help.

A total of eleven months was spent in the field, from February to June in 1947, and from March to October in 1948. Living and dried material was collected and ecological relationships noted at each station and along all roads. The dried material is in the Herbarium of the University of Michigan. Living duplicates were kept in a greenhouse at the Botanical Gardens of the University of Michigan from 1947 to 1949, in order to test the constancy of vegetative characteristics under uniform conditions.

Historical Considerations

The first extensive accounts of desert vegetation and ecology in Trans-Pecos Texas were written by Bray (1901, 1905, 1906). Palmer (1928, 1929), Carter and Cory (1930-31), Cottle (1931, 1932), Muller (1935-36, 1947), Shreve (1939, 1942) and Hinckley (1944, 1947) have contributed substantially to an understanding of the region. The description of the ecology of northern Chihuahua by LeSeure (1945), the report on associations and mammals of mountains in Jeff Davis County by Blair (1940), the vegetational analysis of the Glass Mountains in Brewster

County by Warnock (1946), the account of plant associations in Presidio County by Tinkham (1948), and the discussion of communities by Denyes (1951) are all helpful references. The proposed programs for soil conservation in the Highland and Toyah-Limpia Districts (District Supervisors, 1941a and b) also contain much valuable ecological information. There is, however, little mention of Opuntiae in any of these publications.

Description of Area

The Big Bend Region embraces about 12,000 square miles west of the Pecos River, from a longitude of 102° 20′ to 105°W, and from a latitude of 29° to 31° 5′ N (Fig. 1), and includes Brewster, Jeff Davis and Presidio counties, with much diversity in country rock, resultant topography and vegetation. Most extensive observations during this study were made in Brewster County (with an area of 5935 square miles) which has the greatest range in altitude, from 1400 feet along the Rio Grande to 7835 feet in the Chisos Mountains, and the greatest variation in physiography and plant associations. The Big Bend National Park occupies its southern quarter.

Trans-Pecos Texas falls partly into the Mexican Highland Section and partly into the Sacramento Section of the Basin and Range Province (Fenneman 1931), and is characterized by block mountains, plateaus, bolsons, mesas capped with resistant igneous beds, and few permanent surface streams. It marks the eastern limit of the extensive southwestern desert region.

The geology is well discussed by Hill (1900) and Udden, Baker, and Böse (1916). Mountains occur as groups, series of long tilted blocks, isolated peaks and blocks, and associated with volcanic formations. Separating these are lowland basins and plateau plains. Types of limestone predominate, forming the Dead Horse Mountains, Mariscal Mountain, other scattered areas in the Park, Santiago Mountains, Del Norte Mountains and Glass Mountains. Igneous formations account for the Chisos Mountains and associated outliers, Rosillos Mountains and Davis Mountains with their mesa tongues (Fig. 1).

Because igneous rock under arid conditions is

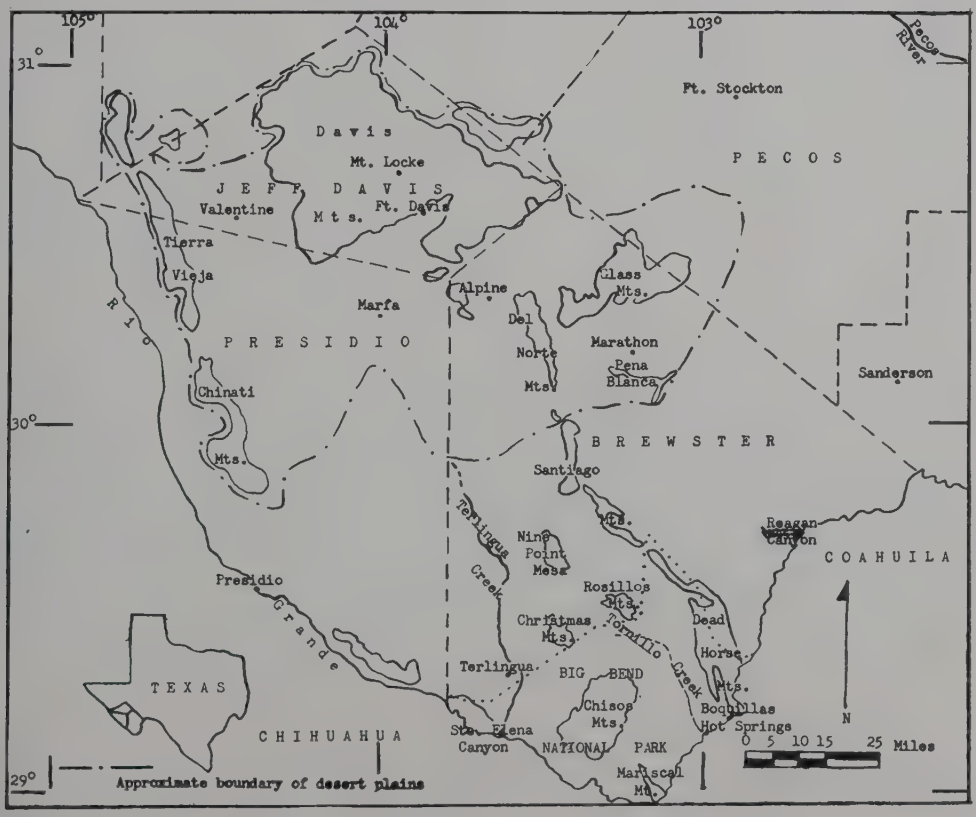

Fig. 1. Base map of Brewster, Jeff Davis, and Presidio counties, Texas.

weathered more rapidly by degradation than is sedimentary rock, soil derived from igneous formations is usually deeper, finer, and looser (Carter and Cory 1930-31). Vegetation is correspondingly more dense and relatively more mesophytic with fewer cacti. In the desert plains life belt on igneous soils, there is a rich variety of annuals and mixed shrubby vegetation (Fig. 2D). *Opuntia engelmannii, O. macrocentra,* and *O. tenuispina* are particularly abundant among the cacti. On similar soils in grassland and mountainous areas of northern Brewster county, *Opuntia imbricata, O. phaeacantha, O. setispina,* and *O. tortispina* are added to the above list.

The shallower and coarser limestone soils have sparser vegetation because of greater porosity and soil continues to develop slowly due to this lack of plant cover (Carter and Cory 1930-31). Taken as a whole, chalky limestone outcrops have a much richer cactus flora than do the igneous soils; there seems to be a definite preference as well as less competition from other plants. In the desert plains life belt, they usually support a barren creosote, creosote-lechuguilla or sotol-lechuguilla vegetation with *Opuntia grahamii, O. grahamii* x *schottii, O. leptocaulis, O. macrocentra, O. phaeacantha, O. rufida* and *O. schottii* as the common subdominants (Figs. 2C and 3B). In grassland and mountainous areas of northern Brewster County, sotol-lechuguilla, short grass-juniper and oak-juniper associations are all found on limestone soil, usually with *O. engelmannii, O. engelmannii* x *phaeacantha, O. imbricata* and *O. phaeacantha.*

Brownish limestone, giving rise to a loose sandy soil, usually has a unique community of *Croton neomexicana* Muell., *Jatropha spathulata* Muell. and *Larrea divaricata* Cav. with *Opuntia macrocentra* and *O. rufida* or *O. tenuispina* as associates.

Southeast of Marathon, the Pena Blanca Moun-

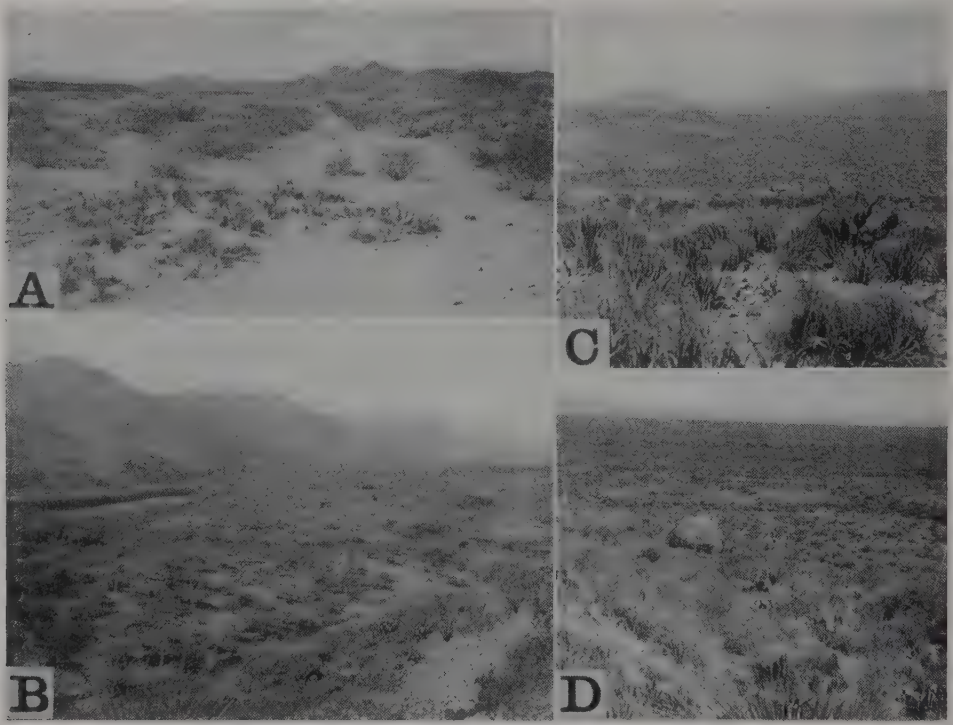

FIG. 2—A. *Opuntia phaeacantha, O. leptocaulis,* and *Echinocereus enneacanthus* form conspicuous clumps on sandy soil south of Rattlesnake Hills, Big Bend National Park.—B. Mesquite thickets (left) along the Rio Grande, creosote bushes with extensive mats of *Opuntia schottii* on a clayey outwash (center) and creosote-lechuguilla on gravelly benches with *O. phaeacantha* (right and background), near the mouth of Reagan Canyon.—C. Southeast of the Chisos Mountains, rough limestone country with creosote-lechuguilla vegetation makes an ideal area for cactus hunting. (*Opuntia macrocentra* in foreground).—D. Scattered plants of *Opuntia phaeacantha* occur with sotol-lechuguilla vegetation (note flower stalks of each) on the igneous rock slope in foreground. The desert flats below support a creosote-tarbush association with *O. engelmannii, O. grahamii, O. imbricata, O. leptocaulis* and *O. macrocentra,* Lone Mountain, Big Bend National Park.

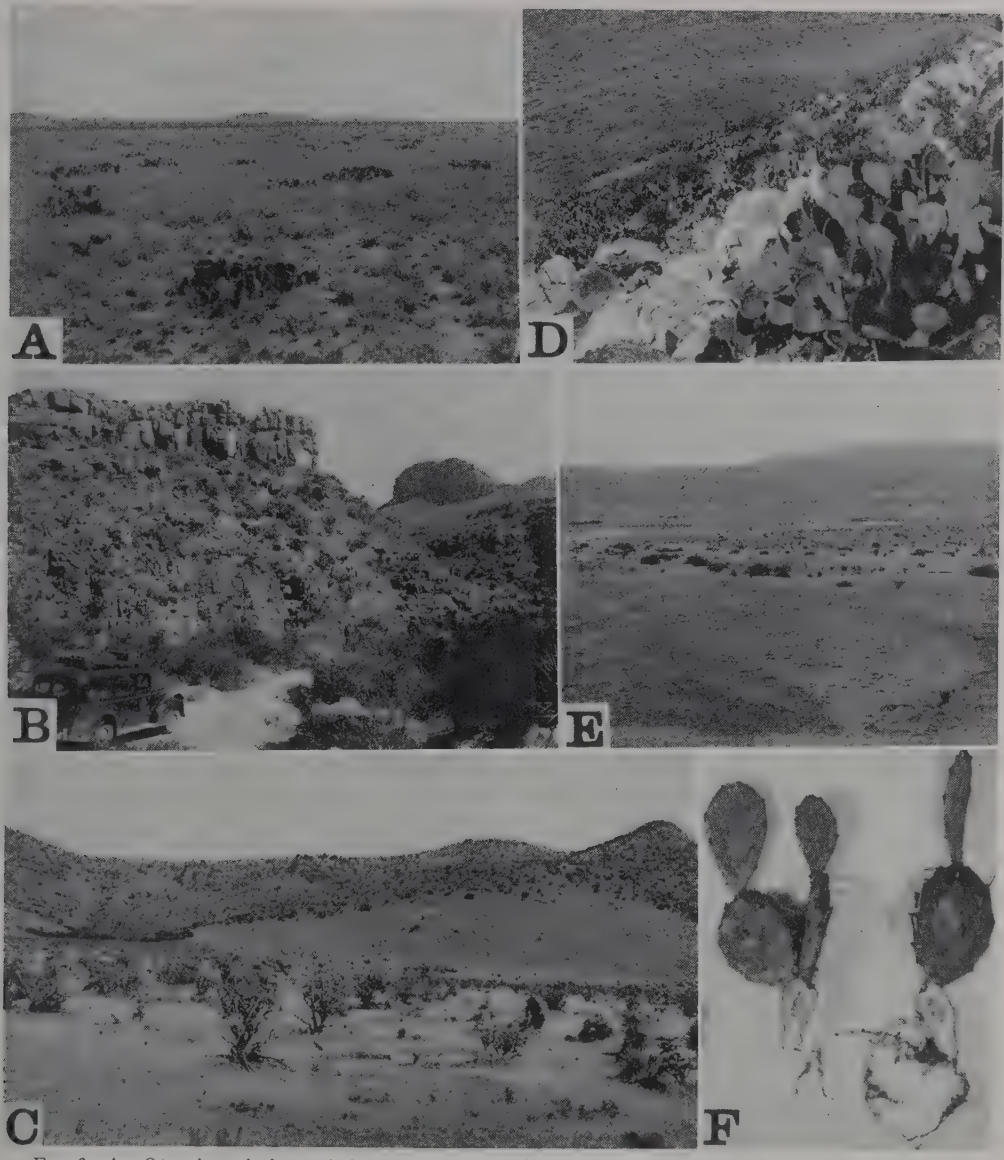

FIG. 3—A. *Opuntia setispina* and *O. tortispina* in a tobosa-platyopuntia association, southeast of Marathon. —B. *Opuntia rufida* reaches its highest development on steep talus slopes and in fractures of limestone cliffs in such deeply eroded country as Reagan Canyon.—C. Short grass-cholla association in a broad valley, in Davis Mountains, with short grass-juniper association in background.—D. Bushes of *Opuntia engelmannii* and *Acacia* spp. on a rocky escarpment slope of the Pena Blanca cuesta formation, short grass-yucca association on flats below.—E. An unusual community of *Coryphantha macromeris, Echinocereus enneacanthus,* and *Opuntia schottii* on a broad clayey wash, east of Mariscal Mountain, Big Bend National Park.—F. Fruit of *Opuntia phaeacantha,* which has proliferated several joints, cut in half to show locule with undeveloped ovules.

tains present an interesting example of thick white chert, a hard porcelain-like rock formed from remains of Paleozoic diatoms and radiolaria. The soil is usually stony and porous. Many bushes of *Opuntia engelmannii* and *O. imbricata* are found on the steep escarpment slopes with *Yucca thompsoniana* and species of *Acacia* (Fig. 3D).

Opuntia engelmannii var. *wootonii* seems to be an edaphically controlled race inasmuch as it occurs only in desert habitats of relatively greater

moisture, such as washes and draws with mesquite.

Opuntia schottii is a species that grows best in clayey situations. A local community of *Opuntia schottii* with *Coryphantha macromeris* (Engelm.) Lemaire and *Echinocereus enneacanthus* Engelm. has developed in a broad clay wash east of Mariscal Mountain (Fig. 3E). The shallow, much blown soil probably limits invasion of other types of vegetation. Near Reagan Canyon extensive mats of *O. schottii* sometimes cover an area of 1.5 square meters among creosote bushes on silty clay. Clumps are much less frequent and are much smaller on the higher gravelly benches with creosote-lechuguilla association, where *Opuntia phaeacantha* is the dominant cactus on sandy loam (Fig. 2B). The mesquite thicket, growing on sand on the left in Fig. 2B, lacks cacti entirely.

Texture of soil and degree of slope affect drainage, which is an important factor governing local distribution of cacti and plant associations.

Steep slopes and flats of coarse detritus afford ideal terrain for a rich and diversified cactus flora since the Cactaceae are well adapted, by their succulence, to arid climatic and edaphic situations. In particular, the Opuntiae, most primitive of the cacti and having therefore the greatest plasticity in response to sharply fluctuating environmental conditions, flourish in abundance where other desert vegetation and other species of cacti are sparse or entirely lacking. In the Big Bend Region, high areas with porous, well-drained gravelly or sandy soils, such as the desert plains south and east of the Chisos Mountains (Fig. 2C) show the best development of cactus populations. Low-lying, clayey, wash areas have few species (*Opuntia leptocaulis* and *O. schottii* are the most common), which would suggest that poor drainage may act as a limiting factor to many species in certain habitats. (Certain other clayey areas, west of the Christmas Mountains and in valleys within those mountains, have such a high soluble mineral content that they cannot support plant cover of any kind. This soil is mined and sold as fertilizer under the name "Min-Sol.") The many talus slopes, cuestas, and canyon walls afford excellent habitats for cacti, especially *Opuntia rufida,* which grows in greatest abundance on the steep limestone cliffs along the Rio Grande and other deeply carved drainage chanels (Fig. 3B).

Warmer and drier southern and western exposures on hills are also suitable habitats for xerophytic plants and Opuntiae are numerically more abundant there than on north- and east-facing slopes.

Tornillo and Terlingua creeks and the Rio Grande are the only permanent streams in Brewster County. Much of the drainage is intermittent and occurs along draws. Torrents of water, coursing down these channels after a heavy storm, often sweep fragments of Opuntiae downsteam where they lodge among rocks or in the tangle of draw vegetation and soon take root. Individuals of *O. imbricata* var. *argentea* and *O. lindheimeri* var. *chisosensis,* both very restricted in range, were found thriving several miles from the main colony along waterways, evidence of an effective means of scattering the population.

Climate

Weather is extremely localized in the Big Bend Region because of the diverse topography. The path of a heavy storm can be marked weeks later by the patches of greener grass. Summers are long and hot with torrential local storms. Most of the rain falls during the hot months of July and August, when the evaporation rate is highest. March and April are among the driest months of the year, yet that is the time when most Opuntiae are setting buds or beginning to flower, seeming to indicate little need for moisture during the budding and floral period. Winters are short and sometimes without killing frosts. Snowfall is light on the grassland plains, somewhat heavier in the mountains. Excessive evaporation is facilitated by high temperatures, sparse plant cover, small amount of rainfall, and continuous winds prevailing from the hot and arid southwest, although there is considerable shifting in direction. Temperatures are subject to great diurnal fluctuation, falling 25°F more or less each night.

The effect of latitude, which increases from about 29° in southern Brewster County to 31° 5′ in northern Jeff Davis County, cannot well be appraised because elevations rise from 1900 to 6000 feet within that distance. *Opuntia grahamii, O. rufida* and *O. schottii* were not found in the desert vegetation east, north and west of the Davis Mountains where elevations decrease again to 4200 feet and lower. It is not evident that latitude limits geographic range of any of the other species of *Opuntia* in the Big Bend Region.

One of the most important factors governing local distribution of the Opuntiae is elevation, through its effect on temperature, precipitation, length of growing season and density of other vegetation. Desert shrub vegetation with spinose, woody and succulent plants, is prevalent in the Big Bend Region at elevations below about 4200-3900 feet, depending upon edaphic conditions. Climatic conditions causing this desert vegetation can be approximated from the weather station at Presidio (Presidio County), elevation 2600 feet,

although temperatures would average higher as one goes downriver through Brewster County to elevations of less than 2000 feet. Twenty years of record (U. S. Weather Bureau 1927-1948) show an average annual precipitation of 9.58 inches, a maximum temperature of 113°F, a minimum temperature of 11° F, and an average growing season of 243 days. The northern and western edges of Jeff Davis County, the southern halves of Brewster and Presidio counties and adjacent Mexico support desert shrub vegetation (Fig. 1). The following forms of *Opuntia* were found only in this type of vegetation: *O. azurea, O. engelmannii* var. *wootonii, O. grahamii, O. grahamii* x *schottii, O. imbricata* var. *argentea, O. macrocentra* var. *minor, O. rufida, O. rufida* var. *tortiflora, O. schottii, O. spinosibacca,* and *O. strigil.*

Grassland vegetation occurs at elevations from about 3900-6000 feet. Climatic data have been recorded regularly at Alpine, Brewster County, elevation 4400 feet, for 17 years. During that period annual precipitation averaged about 15 inches, the maximum temperature was 106°F, the minimum temperature was —2°F, and the growing season averaged 214 days long, with only six years having killing frosts. Forms found almost exclusively in grassland associations are: *Opuntia davisii, O. kleiniae* x *leptocaulis, O. lindheimeri, O. pottsii,* and *O. setispina.*

At high mountain elevations, low temperatures and competition from denser, more mesophytic vegetation (especially grasses) are probably the limiting factors for cacti. Minima of 15°F to —3°F have been recorded over a period of ten years at an elevation of 6780 feet on Mt. Locke where only *O. polyacantha,* that hardy species which extends into Canada, is found. During those ten years, the maximum temperature recorded was 95°F, total annual rainfall averaged 20.60 inches, and the growing season averaged 203 days with three years having killing frosts.

Climatic conditions accounting for woodland associations, at elevations from 5000-7000 feet, range between those recorded at Alpine and Mt. Locke. Forms occurring predominantly in these encinal communities are: *O. lindheimeri* var. *chisosensis, O. trichophora,* and *O. tunicata.*

Variation in amount of annual precipitation at each of these three stations is great, ranging from drought years with approximately 2, 7, and 15 inches of rain respectively for Presidio, Alpine, and Mt. Locke to wet years with about 23, 33, and 36 inches respectively. Note that in drought years the annual total of 15.16 inches at Mt. Locke is less than the annual total of 23.43 inches in a wet year at Presidio. But desert conditions are produced by a combination of edaphic and climatic factors operating over a long period.

Low temperatures are more subject to marked annual deviation than are high temperatures at these desert, grassland, and mountain stations. Since extremes of climatic conditions, particularly low temperatures, are usually the limiting factors for the range of a population, years without killing frosts would allow a population to extend beyond its usual bounds, only to be eliminated again during a severe winter with a minimum below freezing.

During 1947 and 1948, Trans-Pecos Texas endured severe drought which drove many of the smaller ranchers into bankruptcy. Only 4.43 inches of rain fell during 1948 at Johnson's Ranch along the Rio Grande in the Big Bend National Park. Cacti suffered less than most other plants during the dry period but flowered later in the year and less prolifically than usual. The effect of drought is more critical in grassland than in desert areas because the short-grass cover then tends to be less well developed and is often overgrazed, so that Opuntiae can invade and often become well established in a short time with their active vegetative reproduction.

Plant Associations

The Big Bend Region is included in the Chihuahuan Biotic Province (Dice 1943) which is bounded on the east by the Pecos River and extends from southern New Mexico and western Texas into parts of Chihuahua, Coahuila, Nuevo Leon, Zacatecas, and San Luis Potosi.

The approximate outer margin of grassland area is marked by mountains, plateau plains and mesas, all sloping to lower elevations of desert plains (Fig. 1). Scattered patches of xerophytic vegetation occur in the grassland under conditions of considerable biotic disturbance or unfavorable soil, and they enlarge during drought years or in cases of severe overgrazing.

The discussion which follows is based upon the classification by Denyes (1951) which includes thirty-five distinct associations in the Big Bend Region. These plant communities may be used as indicators of differences in country rock, elevation, degree and exposure of slope, drainage, physical and chemical characteristics of soil, and biotic disturbance. In each community one finds characteristic Opuntiae, as summarized in Table I. Abbreviations used for comparative abundance of individuals are defined as follows:

a: abundant and conspicuously visible throughout the association;

f: frequent, scattered throughout, a few visible from any spot;

TABLE I. *Fidelity of Opuntiae with respect to plant associations of Big Bend Region of Texas*

Species	Plant associations	Cañon Biotic District	*Desert Plains Life Belt*	River bank	Baccharis	Willow-Reed	Mesquite	Creosote-Tarbush	Creosote-Mesquite	Creosote-Tasajillo	Arroyo	Tobosa-Grama	Tobosa-Mesquite	Tobosa-Platyopuntia	Tobosa-Tarbush	*Foothills Life Belt*	Chert hill	Sotol-Lechuguilla	Creosote-Lechuguilla	Sotol-Sacahuiste	*Encinal Life Belt*	Oak-Chaparral	Pinyon-Oak-Juniper	Yellow pine-Fir	Grama-Bluestem	Feather grass-Grama	Davis Mountains Biotic District	*Plains Life Belt*	Short grass	Short grass-Yucca	Short grass-Cholla	Short grass-Sacahuiste	Huisache	River walnut	Ayache plume	*Roughland Life Belt*	Rock hill	Juniper-Ocotillo	Sotol-Juniper-Lechuguilla	Juniper-Sacahuiste	Short grass-Juniper	Oak-Chaparral	Oak-Juniper	Pinyon-Juniper
O. azurea Rose																			r																										
O. aavisii Engelmann and Bigelow																												r	r																
O. engelmannii Salm-Dyck				o		o	f	o	r	f	o				f		a	f	f	o		o	f	r	r	r		o	f		r	o	r	o			o	f	o	c	f	o	f	o
O. engelmannii var. *wootonii* (Griff.) Anthony						o	o	o																																				
O. engelmannii x *phaeacantha* Anthony						o	o		r	o					o			o	o									o	o	r		r	r				f	a		o		r	r
O. grahamii Engelmann						o	f	o		r								r	f																										
O. grahamii x *schottii* Anthony							f	o		r								r	o																										
O. imbricata (Haw.) De Candolle							f	o		r	o	r	r	r		f	o	o			o	f					o	f	a	r	r	r				o	o	o	c	f	o	f	f
O. imbricata var. *argentea* Anthony					r													r																										
O. kleiniae De Candolle		r		r	r					r								r									r		r				r										
O. kleiniae x *leptocaulis* Anthony																											r																	
O. leptocaulis De Candolle						o	f	f	a	o	r			o			o	f									r	r		r			r										
O. leptocaulis var. *brevispina* Engelmann							r						r															r						r				o			r			
O. lindheimeri Engelmann							r																					r							r						r	r	r	r
O. lindheimeri var. *chisosensis* Anthony																	r				r	f	o	r	r																		
O. linguiformis Griffiths					r																																							
O. macrocentra Engelmann				o	f	o						o	a				o	a	o									o	o		r					o					f		
O. macrocentra var. *minor* Anthony					r	r																																						
O. phaeacantha Engelmann				o		o	f	f		f							f	f				o	f					r	o	r	r	r	r	r				o	o	f		f	o
O. polyacantha Haworth																																												r
O. pottsii Salm-Dyck											r				r														r	o	r									o		r	r
O. rufida Engelmann							f	r									f	a																										
O. rufida var. *tortiflora* Anthony																	o	o																										
O. schottii Engelmann					r	f	o		r									f																										
O. setispina Engelmann									a			a	r															o	o	r	r	o				o	r			o		r	r
O. spinosibacca Anthony																		r																										
O. strigil Engelmann																																	r											
O. tenuspina Engelmann					r	f	o	r	o	f			o					o				o	f					o	r											r		f	
O. tortispina Engelmann									a			a								r								f	f		o	o								f	o	f	o
O. trichophora Engelmann																																										r		
O. tunicata (Lehm.) Link and Otto																																												r

o: occasional, widely scattered throughout association and only visible from a few places;

r: rare and encountered in a few localities with only one to several individuals there.

Additional observations must be brought out for the following associations:

River bank association:—This habitat seems to be entirely lacking in cacti, doubtless because the usual riparian species such as *Baccharis* and *Phragmites* are better adapted to the high moisture content.

Mesquite association.—In a few areas dunes have been formed by the prevailing southwest winds blowing on shifting sands. Often mesquite is the only vegetation, capping the two- to five-foot mounds; occasionally *Opuntia leptocaulis* grows entangled in the mesquite, deriving both support for its sprawling branches and protection for the seedlings, which are succulent tidbits for desert animals. Such close association probably is explained by process of elimination, since more seedlings under bushes are apt to survive to ma-

turity than unprotected ones. A good example of this community can be found along sandy upper reaches of Tornillo Creek. No cacti were found in thickets of mesquite along the Rio Grande. A grassland counterpart is seen in the occurrence of *Acacia* species and *Opuntia kleiniae* (occasionally also *O. leptocaulis*), in dense thickets along bottomlands of such streams as Musquiz Creek.

Creosote-tasajillo association.—*Opuntia leptocaulis* (tasajillo) and *O. grahamii* often occur as co-dominants where stands of evenly spaced creosote bushes develop on washes with clayey loam. The tasajillo usually grows as much in the midst of the creosote bushes as it does in the mesquite.

Tobosa-platyopuntia association.—This abundance of cacti indicates very favorable edaphic conditions rather than overgrazing. At grassland elevations, tobosa flats are colonized by *Opuntia setispina, O. tortispina,* and occasionally *O. tenuispina* (Fig. 3A). Where tobosa flats have developed in a predominantly desert shrub area, *Opuntia macrocentra* is the platyopuntia co-dominant with occasional plants of *Echinocereus stramineus* (Engelmann) Rumpler. *Opuntia setispina* and *O. tortispina* are entirely restricted to grassland and woodland elevations. Good examples of this desert tobosa flat community are found west of Nine Point Mesa and northwest of Valentine in Jeff Davis County.

Yellow pine-fir association.—At the elevations of 6500-7400 feet where this association is found, *Opuntia polyacantha* is the sole representative of the genus in the Davis Mountains and *O. lindheimeri* var. *chisosensis* is the only representative in the Chisos Mountains.

Short grass-cholla association.—*Opuntia imbricata* becomes co-dominant with short grass in a few circumscribed areas where the species is able to establish itself in great numbers because of overgrazing or especially favorable edaphic conditions, such as on red sandy loam in broad valleys of the Davis Mountains (Fig. 3C). Mesquite is often conspicuously present, indicating greater soil moisture.

River-walnut association.—Opuntiae are of sporadic occurrence along these gravelly stream beds where joints have apparently washed down and ultimately rooted. The plants are usually atypical in appearance because of the relatively mesophytic conditions.

Desert Mountains

The Chisos Mountains in the Big Bend National Park form a semi-mesophytic island, surrounded by desert plains, with sparse xerophytic vegetation. Creosote-tarbush association at 3000 feet elevation, with many plants of *Opuntia leptocaulis* and *O. macrocentra,* is replaced by sotol-lechuguilla association, at about 3900 feet. This desert vegetation yields, at 4500 feet, on the mountain slopes, to oak-chaparral association, which leads up to the pinyon-oak-juniper community with *Opuntia engelmannii, O. imbricata, O. lindheimeri* var. *chisosensis, O. phaeacantha* and *O. tenuispina* as associates. A limited yellow pine-fir association, with *Cupressus arizonica* Greene and *Juniperus flaccida* Schlecht, occurs in sheltered situations above 6500 feet. Only *Opuntia lindheimeri* var. *chisosensis,* an occasional *O. engelmannii,* and a small form of *Echinocereus triglochidiatus* Engelm., are found in this association.

Climatic data for Chisos Basin, only recorded regularly since 1947, were kindly supplied by the Superintendent of the Big Bend National Park and the meteorologist at the U. S. Weather Bureau, Houston, Texas. Annual rainfall in 1947-1948 averaged about 14.5 inches, and temperatures ranged from 5°F to 97°F, but killing frosts were rare.

Grass communities occur only as scattered small meadows in the woodlands; the nearest extensive grassland association lies about 48 miles to the north. Therefore, it is not surprising that *O. davisii, O. lindheimeri, O. pottsii* and *O. setispina* were not found here, although one small specimen of *O. tortispina* was collected in a high meadow known as "the Laguna."

A distinct variety of *O. lindheimeri,* which has been named var. *chisosensis* and has both a yellow-spined and a red-spined form, is the most conspicuous and abundant cactus in the Chisos Mountains. It grows mostly in sunny grass patches rather than in the forest shade and is especially prevalent where natural vegetation is disturbed around Park Headquarters buildings (with *O. imbricata*), the concession cabins, and camp grounds (with *O. engelmannii* and *O. tenuispina*). Several specimens of this variety and its associate, *Echinocereus triglochidiatus,* were found near Oak Springs and Cattail Falls at the northwestern base of the Chisos Mountains, washed down and away from the main population. Possibly these pioneers will extend the distribution away from the mountains.

Nine-Point Mesa is another isolated eminence which arises from desert flats of creosote-lechuguilla vegetation, to a higher plateau of sotol-lechuguilla, and finally abruptly to an elevation of 5100 feet, with a heavily over-grazed oak-juniper association. *Opuntia engelmannii, O. imbricata,* and *O. tenuispina* populate the summit;

however no special forms have evolved here, probably because the area is much less differentiated.

Similar steep masses, such as the sedimentary Christmas Mountains with sotol-lechuguilla association, and the rhyolitic Rosillos Mountains with sotol-yucca vegetation, do not reach high enough elevations to cause isolation effects in distribution of Opuntiae.

Importance of Vegetative Reproduction

Among Cylindropuntiae in the Big Bend Region, all except *Opuntia imbricata* have terminal joints that are easily detached with any slight disturbance of the plant, usually by animals, wind, or rain. These are often carried some distance before coming to rest and, if mature, are capable of withstanding desiccation until roots develop from areoles and take hold wherever the joint is lying. Since the longest spines of the joint are at the terminal end, only the basal end touches ground and the plant is well oriented for continued growth. Woodrats are reported (Riegel 1941) to use detached joints in building barricades around entrances of their burrows; subsequent establishment of these as rooted plants makes the barricades even bigger!

Platyopuntiae all have firmly attached joints but they root easily from areoles of spreading branches which lie along the ground. The branch may be cut off at any point by disease or fragmentation; if there is at least one whole, fairly mature joint a new individual may be started. Cattle, deer, peccary, rabbits, and other animals cause some fragmentation in browsing upon pads. Evidence of browsing on flat joints, esepcially on the spineless forms of *Opuntia engelmannii* and *O. macrocentra,* is common in the Big Bend Region. Cattle usually develop bad mouth sores if they eat joints which have not been prepared as emergency food by singeing. Even old segments of uprooted cactus bases may sprout after months of exposure to desiccation.

Opuntia imbricata, O. kleiniae, O. leptocaulis, O. phaeacantha, O. rufida, O. spinosibacca and *O. tunicata* have fruits which proliferate joints or may even metamorphose into joints, retaining imbedded locules (Fig. 3F). These eventually fall from the parent to start new individuals. Therefore a clone may produce many separate individuals, each alike in genetic constitution. Such ease of vegetative propogation means that sterile hybrids and polyploid forms can be perpetuated in abundance, greatly increasing the number of possible variants among the Opuntiae.

A variety of animals such as cattle, deer, peccary, rabbits, gophers, ground squirrels, mice, birds and ants act as disseminators by feasting upon those cacti with juicy edible fruits. All fruits of this type bear abundant seeds. Riegel (1941), Cook (1942), and Timmons (1942) have reported that rabbits eat the fruits, seeds and all; some seeds pass out in the feces unharmed and are retrieved by ground squirrels who cache or plant them. Percentage of germination is often higher in such cases than for seeds which have not passed through digestive tracts.

Spiny fruits, occurring on *Opuntia grahamii, O. polyacantha, O. schottii, O. spinosibacca, O. strigil,* and *O. trichophora,* and dry fruits, found on *O. davisii, O. imbricata* and *O. tunicata,* are seldom eaten by animals. It is interesting to note that these fruits are mostly sterile as well, so propagation must be predominantly vegetative.

Disease

Insects cause some damage to joints of Opuntiae in the Big Bend Region, but the plants grow fast enough to outpace it. Fungus damage is more evident and more destructive, especially where there are extensive thickets of prickly pears. Actually the thickets may develop in response to disease because plants seem to fruit and vegetate more prolifically when they are badly infected. Disease may cause such distortion in spine formation, often producing more and stronger spines, that the plants become difficult to identify.

Effect of Grazing

Arid grassland plains of the Big Bend Region slope in all directions to desert vegetation (Fig. 1). Cacti do not usually occur to any extent in good stands of native grasses which are best adapted to prevailing climatic conditions and form solid enough cover to crowd out invaders. But with any slight tipping of the balance of environmental factors, such as by over-grazing or severe drought, desert vegetation encroaches rapidly upon grassland. This critical tension exists not only along the margin of the whole grassland region, but also with every patch of desert shrub vegetation that has become established in the plains area. Any break in the solid grass cover that reduces competitive pressure is soon followed by successful invasion of Opuntiae and such other woody desert shrubs as *Microrhamnus ericoides* Gray, *Acacia* spp., *Koeberlinia spinosa* Zucc., and *Flourensia cernua* DC. Establishment of these is especially favored during drought years and Opuntiae, with their effective vegetative reproduction bypassing the longer and more vulnerable seedling stage, may rapidly reach pest proportions. Thus these cacti can well be used as plant indicators since a grassland area with more than the usual few scattered Opuntiae is striking evi-

dence of poor grazing practices with sheepmen largely to blame. The massive *Opuntia engelmannii* and arborescent *O. imbricata* are among the earliest invaders on disturbed rangeland and they become well established in a few years through fragmentation of branches by stock. Eradication of cacti by grubbing and stacking has proven the most effective means but even then many broken pieces take root and grow again. This serious problem of restoring and preserving the natural grass cover through reduction in grazing stock is being met effectively by Soil Conservation groups in several local districts (District Supervisors 1941 a and b).

In desert plains associations, Opuntiae do not seem to compete strongly either among themselves or with other species; large mature plants are often found growing entangled with each other and with other vegetation. Their roots are of a generalized type with an extensive shallow system and a few deep branches so they are able to obtain moisture from any of several levels.

It is doubtful whether Opuntiae can claim any role in control of water erosion since their roots are not consolidated enough to hold the soil. In the matter of wind erosion, individual cacti might serve as windbreaks or nuclei for deposition but there is no evidence that this is effective in modifying the terrain. Desert grasses, and mesquite in some sandy areas, are far more effective in this role. The most important reaction of cacti on the environment is as spiny shelters for other plants, especially grasses which are so important to the rancher. Grasses that are heavily grazed cannot form seed. But grasses growing among branches of cacti, especially the Opuntiae, are left untouched and form full heads; these are often the last stands of good range grass in an area. Succulent seedlings of the Cactaceae themselves often start life in the shelter of a spiny parent or relative, or other desert bush; those germinating in the open are soon eaten or trampled. This may explain why *Opuntia pottsii,* a small species, is usually found in mesquite bushes. Seedlings of *O. imbricata* are the only kind that are seen frequently in the open, perhaps because they seed so heavily.

The Human Factor

One cannot help but notice great thickets of *Opuntia engelmannii* and *O. phaeacantha* around abandoned dwellings in the desert country along the Rio Grande (for example, near Vivianne Mine and Terlingua). These habitats, where there is much disturbance by human trampling, are rapidly invaded by the fast-growing prickly pears; fragmentation doubtless contributes to their rapid colonization, and they tend to overgrow the whole area after buildings are deserted. Masses of Opuntiae around the Park and concession buildings in the basin of the Chisos Mountains illustrate this tendency.

Several large bushes of *O. linguiformis* have become well established in a garden near an abandoned Mexican dwelling on the west bank of Tornillo Creek, one mile north of its joining with the Rio Grande. Since this species has only been recorded as native around San Antonio and is not listed by Bravo (1937) all evidence points to a deliberate introduction which must have taken place more than eight years ago because this whole area was established as a National Park in 1944. Judging by the large size of these bushes, which measured up to 18 dm. in height and about 15 dm. in width in 1948, the introduction was doubtless made much earlier than 1943. The plants are doing well, so it is to be expected that this species will eventually become a part of the natural vegetation, at least in that valley. Flowers are formed so that spontaneous crossing with a native species might very well occur and hybridization might effect a whole wild population in course of time. There is no evidence yet of such modification but it may become an important factor in local evolution.

Transplant Experiment

Much of interest could be learned about cactus responses and speciation through extensive transplant experiments by someone living in such a desert region. A transplant plot was established on the Victor Pierce Ranch in a valley of the Glass Mountains in April of 1947. Climatic conditions at this altitude of 4600 feet are conducive to short grass-juniper association on a loam soil derived from Paleozoic limestone. The valley slopes gently to the northwest and is sheltered by mountains on all sides. Joints of various Opuntiae including *O. imbricata* var. *argentea* and *O. schottii,* all from the southern tip of Brewster County on limestone soils at elevations around 2200 feet, were planted and left until recollected in September, 1948. The intervening winter was severe with a minimum of 0°F recorded at Alpine. Some of the transplants did not form sufficient roots for valid conclusions to be drawn, but survival of *O. imbricata* var. *argentea* (more than 85 miles north of its range) and *O. schottii* (about 43 miles north of its range) does indicate that these forms are not restricted to their southern ranges by sensitivity to low temperatures. Perhaps they have not yet spread as far as grassland areas or else they cannot invade the established vegetation successfully.

Affinities of the Opuntiae

Floristic affinity with short-grass plains of the Kansan Province and the pinyon-juniper woodland of the Navahonian Province, both adjoining on the north, is evinced by such grassland and encinal species as *Opuntia davisii, O. polyacantha, O. tortspina* and *O. trichophora.* These may have migrated in either direction along the Guadaloupe, Delaware, Apache, and Davis Mountains, or adjoining valleys and high plateaus.

The Stockton Plateau forms a natural bridge between the Basin and Range Section, Edwards Plateau, and lower Coastal Plain Section (Fenneman 1931) so that *Opuntia lindheimeri* and *O. schottii* are found with arid grassland, scattered shrubs and low trees in the Comanchian Province of eastern and southern Texas, as well as in the Big Bend Region. None of the Trans-Pecos plants of typical *O. lindheimeri* achieve the massive size of those farther east, which suggests that the species is near the limits of tolerance to some factor in the Big Bend Region, although it has given rise to an endemic variety in the Chisos Mountains.

Ranges of *O. azurea, O. kleiniae, O. pottsii, O. rufida, O. schottii, O. setispina, O. tunicata,* and possibly the new species *O. spinosibacca,* extend from adjacent Mexico (part of Chihuahuan Province) across the Rio Grande northward into desert and grassland associations. These could have migrated along mesa tongues of grassland which extend southward from latitude 30° and along desert valleys sheltered by the mesas.

The Apachian Province of grassy high plains and mountains with encinal and montane vegetation is contiguous on the west. Distributional areas of *O. engelmanii, O. macrocentra,* and *O. tenuispina* are approximately coincident with boundaries of the Chihuahuan and Apachian Provinces, showing an interchange in those floras.

Correlation of Species Area with Ecological Variability

Such species as *O. setispina, O. rufida,* and *O. strigil* have relatively small ranges of distribution in North America. The latter two are also among the most restricted and sparse in local distribution. Although *O. strigil* is very abundant west of the Pecos River in Terrell County and on limestone ridges in Pecos County, it was not found in the Big Bend counties where there are similar habitats. It may be a relatively new species in its center of origin and has yet to spread, it may be a relict population in its last stand, or it might be highly specialized physiologically, restricting its occurrence to a few localities with certain edaphic conditions. *Opuntia rufida* and its variety *tortiflora* grow in great numbers on limestone cliffs and cuestas along the Rio Grande and are also common on gravelly plains south and east of the Chisos Mountains. From these mountains northward, however, the plants are of sporadic occurrence only, leading to the limit of range near where transition to grassland occurs. *Opuntia setispina* is more adaptable, occurring abundantly throughout grassland and into woodland vegetation.

Opuntia davisii, O. kleiniae, O. lindheimeri, and *O. pottsii* have somewhat larger distributional areas but all are rare thoughout the Trans-Pecos area, indicating a high degree of ecological restriction for they are scattered enough to offer ample opportunity for large populations.

Opuntia engelmannii, O. imbricata, O. leptocaulis, O. tenuispina, and *O. tortispina* are widespread in the United States and Mexico and are also common in many habitats in the study area. *Opuntia polyacantha* and *O. trichophora* likewise range over much of western United States but have not previously been reported so far south. Here they are very rare, occurring only in a few sheltered situations with montane vegetation.

Opuntia spinosibacca was found only around Boquillas and in the driest situations there. It has either migrated across the Rio Grande at Boquillas from Mexico, is just beginning to spread from its center of origin there, or is a relict population.

This correlation between extensive general distribution and widespread local distribution, and between restricted general distribution and limited local occurrence, indicates considerable variation in degree of adaptability among these Big Bend Opuntiae. Those which are found under many different conditions in the area appear to have flexible ecological requirements which enable them to survive over greater expanses of territory in North America than those which are specialized to one or a few habitats in the study area.

Opuntia tunicata presents an interesting problem in disjunct distribution. Grisebach (1866) and Carabia (1937) list it in Oriente, Cuba, as does Brother Lenée on herbarium sheets in the United States National Herbarium. Bravo (1937) gives the distribution as, ". . . abundantly throughout the Mesa Central and as far as South America." Herbarium specimens from Mexico have been collected in Saltillo, Coahuila, Mexico D.F., Puebla, San Luis Potosi, Zacatecas, and "Cerro de los Banos" (state unknown). A small colony is now well established just below some high limestone cliffs at about 4050 feet elevation on the southeastern slope of an outlier east of the Glass Mountains. Such distribution, guided by

a cliff barrier, suggests dissemination by grazing animals which brush off the exceedingly spiny and easily detached joints and carry them along in their pelage. None of the clumps approach the five to six decimeter height recorded for Mexican collections; frequent disturbance by grazing stock, as well as by wild animals, may account for this low stature. Other individuals scattered in pinyon-oak-juniper vegetation above the cliffs and further up the hill, indicate that the species is rapidly spreading.

Possible means of migration of *O. tunicata* from locations in Mexico and the West Indies offer interesting speculations. Grazing animals may have played an important role in transporting fragments of plants from place to place. The colony is about half a mile from the Marathon-Ft. Stockton road which makes human introduction seem improbable. Since intervening regions are not well explored it is possible that the distribution is actually more continuous than it appears.

Growth of Opuntiae Under Controlled Conditions

Opuntiae collected in the field and grown under the controlled conditions of a greenhouse often produce new joints lacking the variations developed by those plants in their native habitats. Old joints differing markedly in spine formation or unusual joint shapes may produce new growth that is identical in appearance. Joints that are diseased may form healthy new growth which looks just the same as typical members of the species. Color and form of young spines become taxonomically dependable under such conditions. This experimental method then is a most useful one for identification of the many forms of this plastic genus found in the field.

For instance, a specimen of *Opuntia imbricata* var. *argentea* has produced a number of new joints which are more abundant, arise at more acute angles and are spinier than joints of the typical *O. imbricata* growing under the same conditions in the greenhouse. Such evidence obviates the possibility that the silver-spined form might be just an edaphic or climatic response; the new characteristics must be genetically inherent in this variety.

Joints of the Platyopuntia, *O. trichophora,* grown at the Botanical Gardens since 1947, have formed new shoots with cylindrical cross-section, indicating the degree of plasticity that these plants have in response to environmental changes.

A much longer period of experimental growth would be desirable, especially since Opuntiae do not flower readily under glass and seedlings take several years to develop mature characteristics, so that hybridization tests would be a long term project.

Opuntia seeds germinate most readily when fresh; they should be planted as soon as possible after collection. Once dried out, they usually require scarification to induce germination. Seeds of a number of species, which seem to depend on vegetative reproduction entirely, are sterile.

Evolutionary Implications

The Opuntiae present a challenging problem in taxonomy with the stem-like nature of their fruits, their marked response to environmental conditions, and prevalence of asexual reproduction. *Opuntia engelmannii, O. phaeacantha,* and *O. tenuispina* can be interpreted each as a polymorphic complex, having a continuum of intergrading variants within each species. This continuum may best be represented as a curve with minor peaks where numerous individuals with distinctive combinations of characteristics, are clustered. These peaks are separated by wide valleys with variants whose characteristics lie between one extreme, or peak, and the next peak, where another set of characteristics tends to occur in many individuals in a recognizable combination.

Populations of *Opuntia phaeacantha* in desert grasslands and encinal situations of this region afford a good example of this type of variation. Forms from the desert are spreading ascending bushes with ovate pads and many reddish-brown spines. In grassland, the bushes may be less branched but bear large joints, with fewer, stronger and redder spines; Engelmann recognized these as the variety *major.* At encinal altitudes, *i.e.* in the Del Norte Mountains, the plants are prostrate with fewer and grey to brown spines.

The trend in the study of the genus has been toward lumping these varieties into a broadly defined species. Where there is no clear break in gradation this treatment is the most practical one for most purposes. But one must not lose sight of the role that variants play in the complex; namely, that of presenting diverse material which may, through isolation, produce new taxonomic entities.

Forms intermediate between *Opuntia grahamii* and *O. schottii,* and which vary in degree of resemblance to one or the other, have been interpreted in this study as hybrids, because the variation has been expressed around a mean between the two parents rather than as a continuous gradation from one to the other. Hybrids between *O. engelmannii* and *O. phaeacantha* likewise form a highly variable population whose representatives

do not fit into either species but range around a mean between them. A few hybrids between *O. kleiniae* and *O. leptocaulis* were also found at one station.

If mutations occur, those affecting physiology may be much more significant than those affecting morphology, especially adaptations in water metabolism and changes in time of flowering period which render genetic mixture with the parent type impossible.

Taxonomy of this genus would be much clarified by a complete analysis of chromosomes; special techniques must be employed to overcome the problem of high mucilage content in the cells. Time was lacking in the study for such work, so it is not possible to state if any polyploids exist, as shown for *Opuntia polyacantha* by Stockwell (1935). The *O. phaeacantha* complex does suggest that sort of relationship.

Populations which seem to have little genetic variability, *i.e.* most of the Cylindropuntia group in this region, usually have greater habitat restriction because they lack variants adapted to diverse environmental conditions. Evolution proceeds more slowly under constant conditions than if segments of the population were being subjected to a great variety of conditions. As populations of a genetically variable species spread out, forming a number of variants adapted to more and more habitats, the possibility grows that some fraction of a population will become modified enough or isolated enough that a new species will evolve.

Endemism

The general flora of the Big Bend Region extends north to southern New Mexico and south far into Mexico, and the whole area has marked diversity in topography, affording many small habitats separated by barriers of mountains or desert conditions, which sets an ideal stage for endemism.

Each of the six varieties of Opuntiae in this area (Table I) may be thought of as extreme selections from interbreeding polymorphic populations, forming prevailing populations by rapid propagation in favorable habitats. Any especially adapted types which segregate out and attain dominance in a particular area, are potential endemic species. It must be remembered that in *Opuntia* the establishment, as ecological dominants, of especially adapted types—hybrids, mutants or polyploids—is much facilitated by dispersal of joints and subsequent vegetative propagation.

Summary

Opuntia populations were studied in Jeff Davis, Presidio, and Brewster counties, with the latter receiving the most detailed consideration. Climate of the Big Bend Region is typically arid with high evaporation, low precipitation with the peak during the hottest summer months, and widely fluctuating diurnal temperatures. Great variety of topography and resultant localization of soil and moisture conditions have produced a corresponding diversity of habitats. These are occupied by at least thirty-six plant communities of which four feature cacti as follows:

creosote-tasajillo, *Coryphantha-Opuntia,*
tobosa-platyopuntia, and short grass-cholla associations.

Thirty-one species, varieties and hybrids of *Opuntia* are found in the area.

Elevation, through its concurrent effect on climate, and drainage constitute the most evident factors in local distribution of Opuntiae. Type of country rock, texture of soil, degree and exposure of slope, and amount of grazing are also determining factors. Therefore, local distribution of Opuntiae can be closely correlated with the plant associations since they are an accurate index to topographic and climatic conditions. The richest cactus flora is developed on high, gravelly desert plains in the Big Bend National Park. Vicissitudes of chance, such as transportation by torrential drainage or by animals, account for occasional isolates not in the usual habitats. Desert eminences have produced well-defined races and disjunct distributions of Opuntiae through isolation effect.

Prevalence of vegetative reproduction among Opuntiae is a very significant factor explaining their: 1) rapid invasion and establishment in newly available habitats, 2) general ubiquity, and 3) variety of forms. Animals browsing and eating fruits, overgrazing, and disturbance around habitations stimulate increase in local populations of Opuntiae. Woody vegetation, especially *Opuntia engelmannii* and *O. imbricata,* is increasing and invading grassland in much of Trans-Pecos Texas because of severe overgrazing.

Proximity of four adjacent biotic provinces has made the Big Bend Region a meeting ground for woodland, high plains, arid grassland and desert forms of Opuntiae. Most of the Opuntiae with restricted distribution in the Big Bend Region also have a relatively small area of general distribution, indicating low degrees of ecological variability or relatively new species. *Opuntia tunicata* offers an example of disjunct distribution

far from its closest recorded occurrence at Saltillo, Coahuila, in Mexico.

Joints of Opuntiae which look very different in the field may, when grown in a greenhouse, produce new joints lacking such differences. This shows that those dissimilar forms all belong to one taxonomic entity since their new growth is identical. Three of the species are considered as polymorphous complexes, having intergrading variants within each group. These offer a wealth of material for isolation, subsequent race development and possible speciation in this region of severe climatic fluctuations and many physical barriers. Three hybrids found in the area contribute additional variation in local populations.

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CELL CONTENTS OF NITROGEN AND PHOSPHORUS AS A MEASURE OF THEIR AVAILABILITY FOR GROWTH OF *MICROCYSTIS AERUGINOSA*[1]

GERALD C. GERLOFF AND FOLKE SKOOG
Department of Botany, University of Wisconsin, Madison, Wisconsin

Problems arising from excessive growths of phytoplankton in fresh water lakes have become intensified through the discharge of nutrients in sewage effluents and industrial wastes into these bodies of water. It has been proposed that the amount of growth might be reduced by removal of critical essential elements before the effluents are released. The effectiveness of removing a particular essential element will depend on the extent to which it is normally a limiting or critical factor for algal growth, as obviously removal of a nutrient that is already present in a lake in abundant supply cannot produce the desired results.

Reliable measurements on the degree to which a specific element is actually limiting the growth of algae in nature are difficult to obtain. They must be based on determinations of the availability of the element to individual species in relation to their quantitative nutritional requirements. Granting that algae are capable of absorbing elements from water to the limits of detection by chemical procedures, still the simple method of estimating nutrient supplies by analysis of water collected from the area in which the algae are present may be of little value in this connection for the following reasons: (1) the total supply of a nutrient element is dependent on the total volume as well as the concentration of the solution from which it is absorbed, and this effective volume will vary with the extent to which the algae are moved about and come in contact with different volumes of water. This fact becomes particularly important when it is considered that the composition of the water may vary greatly from the top to bottom layers, especially in lakes that stratify, in a particular area and from one area to another, and that the algae collected in one place may be derived from areas scattered widely with respect to both depth and surface location. (2) The concentration of nutrients in the water may not reflect the total supply in that water over a period of time but rather the level reached as a result of continuous withdrawal by organisms and renewal by inflow and release from less available forms, or, in the case of nitrogen, perhaps also from biological fixation by certain organisms. These difficulties in determining available supplies of nutrients for algal growth are essentially similar to those encountered in determining nutrient availability to crops in terms of soil analyses but in some respects are accentuated by the high degree of independent movement of both the organisms and the water.

In recent years, methods of evaluating nutrient availability to plants in terms of tissue composition have been developed (Lundegårdh, 1951; Ulrich, 1952; Thomas, 1945; Goodall and Gregory, 1947) and have been extensively employed for crop production. It has been found that, regardless of the composition of the external medium and other factors which may affect the uptake of a certain element, a fairly definite concentration (critical level) of that element must be maintained in the tissue to permit optimum growth. The tissue content of the element may continue to increase far above this critical level when it is in abundant supply, but the excess (luxury consumption) has little effect on growth. This paper presents a comparable procedure for evaluating the supply of nitrogen and phosphorus, the elements generally considered most likely to limit phytoplankton growth, to *Microcystis aeruginosa* in lake waters and includes preliminary results obtained in its application.

CULTURE MEDIUM AND EXPERIMENTAL PROCEDURE

For this work, the culture medium employed in previous experiments with *Microcystis aeruginosa* (Gerloff *et al.* 1952) was modified to contain approximately twice the minimal amounts of the essential elements, except iron which was changed to triple the minimal concentration, necessary for maximum growth during a 14-day period. The concentrations, as p.p.m., of the major essential elements were N, 20.4; P, 0.45; K, 2.25; Mg, 0.25; S, 1.65; Ca, 0.25; and Fe, 0.28. As shown in Table I, the use of this solution, even with phosphate concentrations considerably great-

[1] This work was supported in part by a research grant from the Division of Research Grants and Fellowships of the National Institute of Health, United States Public Health Service, and in part by the University Research Committee on funds from the Wisconsin Alumni Research Foundation.

The authors wish to thank Miss Betty Robinson, Technical Assistant, and Mrs. Margaret Hirozawa, Technical Assistant, for their aid in carrying out these experiments.

er than employed in subsequent experiments, avoids the formation of phosphate precipitates which occur on autoclaving the medium used in earlier experiments and which would interfere with determinations of the phosphorus contents of the cells.

TABLE I. *Phosphorus retained in solution in autoclaved modified Chu No. 10 and 2x minimal media containing various levels of added phosphorus*

Treatment	Culture Medium	P.p.m. P added	P.p.m. P in solution
A	Modified Chu soln.	0.45	0.05
B	" " "	1.80	0.45
C	" " "	3.60	0.60
D	" " "	7.20	2.50
E	" " "	14.40	10.00
F	2x Minimal soln.	0.45	0.47
G	" " "	1.80	1.88
H	" " "	3.60	3.75
I	" " "	7.20	7.57
J	" " "	14.40	14.50

The algae were cultured in 500-ml. Erlenmeyer flasks containing 200 ml. of nutrient solution and were placed under continuous fluorescent light of approximately 100 ft.-candles intensity. Cells for chemical analyses were separated from the medium by a Foerst centrifuge and, after being washed to remove traces of the culture medium, were dried to constant weight at 63° C. in tarred weigh-bottles. The dried algae were washed into 100-ml. Kjeldahl flasks and, after evaporation of the water, total nitrogen was determined by a semi-micro-Kjeldahl procedure. Total phosphorus was determined by a stannous-reduced phosphomolybdic blue color method on samples wet-ashed in a mixture of perchloric, nitric, and sufuric acids. All data reported are average results of duplicate determinations, and all experimental results have been confirmed in separate experiments.

The amount of growth obtained with various treatments was determined by centrifuging the algae from 100-ml. aliquots, washing once in distilled water, and drying to constant weight. By centrifugation at high speeds, it was possible to separate the algae from the nutrient solution without the addition of $Al_2(SO_4)_3$ as employed in earlier work (Gerloff *et al.* 1950).

CHANGES IN CELL CONTENTS OF NITROGEN AND PHOSPHORUS WITH STAGE OF GROWTH

The first experiment was carried out to determine if the nitrogen and phosphorus contents of *Microcystis* would vary with increase in growth of the cultures, even though the nutrient solution contained greater amounts of these elements than would be absorbed by the algae during the entire culture period. A large number of cultures was prepared containing 2.25 p.p.m. phosphorus and 23.8 p.p.m. nitrate-nitrogen. The algae from fifty flasks were harvested six days after inoculation and from additional smaller numbers of flasks subsequently every other day until the end of the experiment.

The yield and composition of the algae are presented in Table II and the changes in nitrogen and phosphorus contents with increasing age of the cultures are plotted in Figure 1. The curves clearly show marked but approximately proportional decreases in the nitrogen and phosphorus percentages in the cells. Phosphorus decreases from a high value of 0.83 per cent (after 6 days) to 0.34 per cent (after 20 days) and the nitrogen decreases correspondingly from 9.0 to 3.8 per cent.

TABLE II. *Changes in the total phosphorus content, total nitrogen content, and amount of growth of* Microcystis aeruginosa *at successive stages of a 20-day growth period*

Days after inoculation	% P in algae	% N in algae	Mg. growth per liter
6	0.83	8.96	37
8	0.76	9.15	71
10	0.66	8.17	139
12	0.53	6.71	208
14	0.46	5.41	273
16	0.38	4.62	343
18	0.35	4.11	384
20	0.34	3.77	399

The culture solution contained 23.8 p.p.m. NO_3-N and 2.25 p.p.m. P.

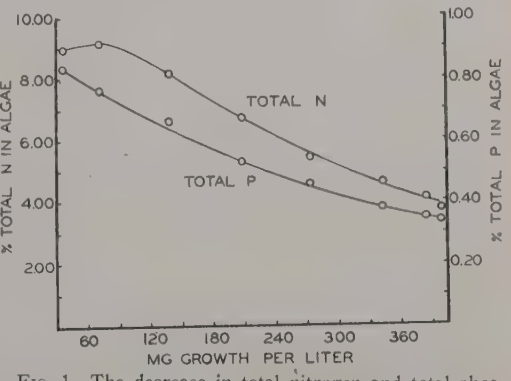

FIG. 1. The decrease in total nitrogen and total phosphorus contents of *Microcystis aeruginosa* as the amount of growth in cultures increased during a 20-day period.

In view of these decreases, the stage of growth must be considered in comparison of nitrogen or phosphorus contents in algae from different experiments. The decreases may be due to increases in the sheath material and storage products as the cells mature. They were not due to exhaustion of the supply of the elements, as shown by analyses

of the culture media at each harvest date. Even after 20 days, the nutrient solution contained 1.10 p.p.m. phosphorus and 7.3 p.p.m. nitrate-nitrogen that had not been absorbed by the algae. It had been found previously that with suboptimal amounts of either nitrogen or phosphorus, *Microcystis* so completely removes these elements from the medium that they cannot be detected by chemical tests.

Figure 2 shows the weight increase of the cultures during a 20-day period. The various stages of a typical growth curve may be distinguished. It is apparent that cultures harvested after 10 to 14 days, the culture period employed in the experiments to be reported, were in the logarithmic phase.

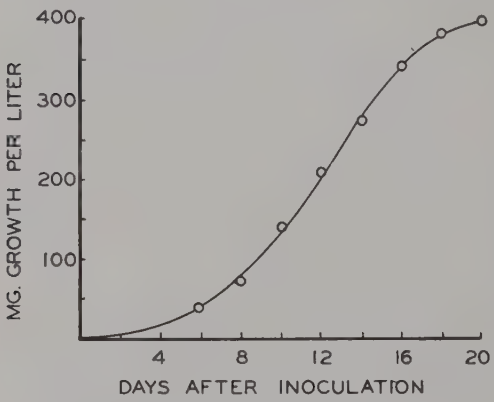

FIG. 2. Growth curve of *Microcystis aeruginosa* during a 20-day culture period in 2x minimal solution.

CHANGES IN COMPOSITION AND YIELD WITH VARYING LEVELS OF NITROGEN OR PHOSPHORUS IN THE CULTURE MEDIUM

Nitrogen: Figure 3 shows the variations in total nitrogen content and yield of *Microcystis* cultured for 14 days in nutrient solutions to which from 5.1 to 20.4 p.p.m. nitrate-nitrogen had been added. The curves clearly show that whereas both the nitrogen content and yield of the algae increase with increasing levels of nitrogen in the solution until each attains a maximum value, these maxima are reached at different external concentrations, the values being 8.0 p.p.m. for yield and 17.0 p.p.m. for nitrogen content. The nitrogen contents in the cells at these points are 4.0 and 7.7 per cent respectively. Thus, although there is a broad range in nitrogen content of the algae, 3.2 to 7.7 per cent, depending on the amount present in the medium, through a major portion of this range, 4.0 to 7.7 per cent, the yields are constant and the increase in nitrogen content of the cells represents luxury consumption of this element.

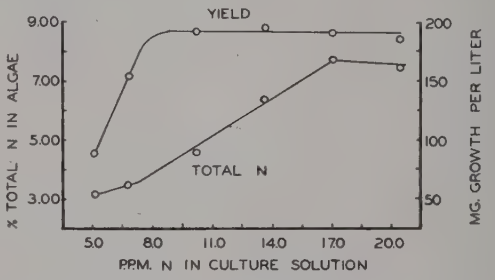

FIG. 3. Growth and total nitrogen content of *Microcystis aeruginosa* cultured for 14 days in nutrient solutions containing various levels of NO_3-N.

Phosphorus analyses, Table III, were made on cells containing various levels of nitrogen to determine concomitant variation in this element. There was only a slight increase in the phosphorus content, from 0.43 to 0.57 per cent, associated with the more than two-fold increase in nitrogen. It will be shown later that even the low value of 0.43 per cent is far in excess of the critical value for phosphorus.

TABLE III. *The total nitrogen content, total phosphorus content, and yield of* Microcystis aeruginosa *grown for 14 days in culture solutions containing varying levels of* NO_3-N

Treatment	P.p.m. N added	% N in algae	% P in algae	Mg. growth per liter
A	5.1	3.16	0.43	88
B	6.8	3.47	0.43	154
C	10.2	4.59	0.43	192
D	13.6	6.39	0.54	195
E	17.0	7.72	0.57	191
F	20.4	7.43	0.56	186

The culture solution contained 1.8 p.p.m. P.

Phosphorus: Experiments were next carried out to determine the change in phosphorus content and yield of *Microcystis* with increasing amounts of phosphorus added to the nutrient solution. The results in Table IV were obtained after a 14-day culture period. The yield increases with the external supply of phosphorus while the cell content remains at approximately 0.12 per cent; thereafter, it remains constant even though the phosphorus content of the algae continues to increase linearly to a maximum of 0.46 per cent (Fig. 4). Thus, there can be almost a four-fold increase in phosphorus content, 0.12 to 0.46 per cent, without a significant change in yield. This represents an even wider range of luxury consumption than in the case of nitrogen.

TABLE IV. *The total phosphorus content and yield of* Microcystis aeruginosa *cultured for 14 days in solutions with varying levels of phosphorus*

Treatment	P.p.m. P added	% P in algae	Mg. growth per liter
A	0.10	0.12	133
B	0.15	0.11	181
C	0.25	0.16	203
D	0.40	0.22	215
E	0.60	0.35	207
F	0.80	0.43	217
G	0.90	0.42	221
H	1.00	0.45	213
I	1.20	0.46	221

The culture solution contained 20.4 p.p.m. NO_3-N.

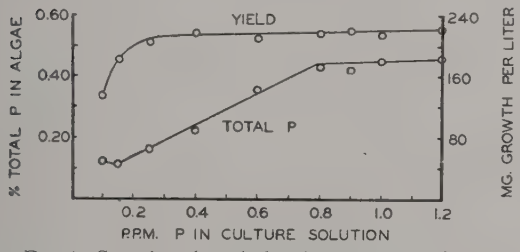

FIG. 4. Growth and total phosphorus content of *Microcystis aeruginosa* cultured for 14 days in nutrient solutions containing various levels of phosphorus.

The variation in phosphorus content is not associated with appreciable variation in nitrogen, for cells from treatments D and I, with 0.22 and 0.46 per cent phosphorus respectively, contained 6.93 and 6.84 per cent nitrogen.

The relationships expressed by the curves in Figure 4 have been confirmed in an experiment with the culture period reduced from 14 to 10 days. As shown in Figure 5, growth was again practically constant over a major portion of the curve where the phosphorus content of the cells is still increasing. However, the maximum yield of algae is reduced from 221 mg. to 101 mg. per liter, the minimum phosphorus content of the algae for maximum growth is increased from 0.12 to 0.20 per cent, and the maximum phosphorus content is increased from 0.46 to 0.67 per cent. The results of an additional experiment, not presented here, showed that comparable changes in nitrogen contents occur when the culture period is shortened. These differences are in agreement with the results presented in Figure 1 showing that both nitrogen and phosphorus contents decrease with the length of the culture period.

NITROGEN AND PHOSPHORUS CONTENTS OF *Microcystis aeruginosa* FROM LAKE BLOOMS

The results of the various experiments are summarized in Table V. With this information, it

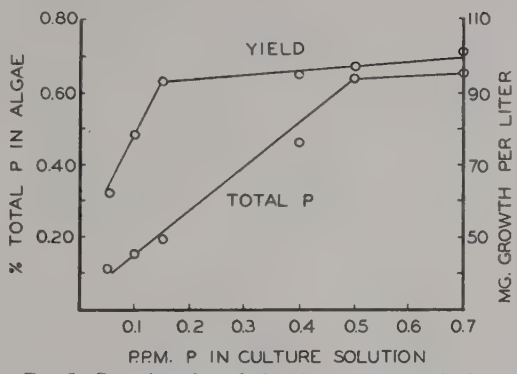

FIG. 5. Growth and total phosphorus content of *Microcystis aeruginosa* cultured for 10 days in nutrient solutions containing various levels of phosphorus.

should be possible to estimate from analyses of field samples the extent to which nitrogen or phosphorus might be limiting growth of *Microcystis* under natural conditions. For example, a cell content below 5.0 per cent nitrogen or 0.20 per cent phosphorus (conservatively high critical levels) would indicate that the growth of the algae is in proportion to the available supply of the element in question, and that an increase in the amount of growth would require a higher rate of supply of the element. Cell contents above these critical levels, on the other hand, would indicate that the elements are being supplied at faster rates than utilized and therefore are not limiting growth.

TABLE V. *Summary of minimum and maximum percentage contents of nitrogen and phosphorus in range of constant yields of* Microcystis aeruginosa

Expt.	Element varied	Growth period, days	Max. growth, mg/l.	Min. and max. per cent of element in range of max. yields	
1. Fig. 3	N	14	195	4.0	7.7
2	N	12	120	4.6	9.4
3. Fig. 4	P	14	221	0.12	0.46
4. Fig. 5	P	10	101	0.20	0.67

Samples of *Microcystis* from heavy blooms in lakes in the vicinity of Madison, Wisconsin, were collected for analysis. The algae were gathered with a plankton net and then immediately suspended in distilled water. Upon return to the laboratory, aliquots of the suspensions were removed and dried to constant weight for nitrogen and phosphorus determinations. With this procedure, contamination of samples with nitrogen or phosphorus from the lake water was reduced to a minimum and any nitrogen or phosphorus leached from the cells was recovered in the aliquots dried

for analysis. All samples were examined under the microscope and only those that were nearly pure *Microcystis* were used.

The results of total nitrogen and phosphorus determinations on seven samples collected from three different lakes are presented in Table VI.

TABLE VI. *The total nitrogen and total phosphorus contents of samples of* Microcystis aeruginosa *collected from heavy blooms in lakes in the vicinity of Madison, Wisconsin*

Sample	Date collected	Sample source	% total N in algae	% total P in algae
A	7-6-52	Spaulding's Pond	7.76	0.98
B	8-6-52	" "	6.34	0.58
C	8-25-52	" "	6.22	0.61
D	9-3-52	" "	6.95	0.62
E	8-6-52	Lake Waubesa	6.19	0.52
F	9-4-52	" "	5.64	0.64
G	9-3-52	Grass Lake	8.68	0.87
		Average values	6.83	0.69

By reference to Table V, it is immediately obvious that both the nitrogen and phosphorus contents of all these samples are considerably above the critical levels for maximum growth established in the laboratory experiments. However, the average nitrogen content of 6.83 per cent is considerably below the maximum content obtained experimentally, whereas the average phosphorus content of 0.69 per cent is even slightly higher than the maximum laboratory values of 0.67 per cent (Table V). Since, relative to need, phosphorus is obviously present in greater excess, a more accurate estimate of the adequacy of nitrogen supply to the lake algae might be obtained by comparing the nitrogen content of the samples with that of cultured algae with equally high phosphorus content. This correction can be made without regard to the minimum values by reference to the curves in Figure 1. The nitrogen content of algae with an excess nitrate supply and a phosphorus content of 0.69 per cent (the average value of the lake algae) is 8.7 per cent. This corresponds to a yield of 110 mg. per liter and is in satisfactory agreement with the results of the second experiment in Table V in which the maximum yield was 120 mg. per liter and the maximum nitrogen content was 9.4 per cent. The critical value actually observed in this experiment was 4.6 per cent which is well below the observed nitrogen content of the lake samples.

Actually, since the critical values seem to remain relatively constant, a correction of the above type is of interest principally in determining the extent to which an observed nitrogen content above the critical level represents a reserve supplying power not actually utilized for the growth of the algae in the lakes. Thus, in the above case, the reserve supplying power of nitrogen in the lake water is expressed by the fraction:

$$\frac{\text{Sample content—Critical level}}{\text{Maximum content—Critical level}} \text{ or } \frac{6.8 - 5.0}{8.7 - 5.0} = \frac{2}{3}$$

This method of estimating supplying power in terms of the degree of luxury consumption by the algae of a particular essential element may provide only an approximation, but it does take into account the marked normal variations in maximum cell contents of the element. Similar corrections in phosphorus content could be made in case nitrogen were present in the samples in greater excess than phosphorus.

Utilization of Stored Nitrogen and Phosphorus

The results presented above indicate that algae might absorb sufficient nitrogen or phosphorus from an environment containing relatively high concentrations of these elements to permit continued growth in an environment where they are deficient. The nitrogen and phosphorus would be distributed in successive cell divisions until one of the elements was reduced to its critical value. An experiment was carried out to determine the extent to which this might occur. *Microcystis* was cultured in solutions containing various levels of either nitrogen or phosphorus, as indicated in Table VII, and after 12 days the cells were centrifuged from the solutions and transferred to media lacking either nitrogen or phosphorus. To avoid carry-over of traces of nitrogen or phosphorus from the original medium, the cells were rinsed in a solution lacking both of these elements. The yields obtained in an additional 12-day growth period were then determined.

TABLE VII. *Growth of* Microcystis aeruginosa *in culture solutions lacking nitrogen or phosphorus after initial growth in solutions containing various levels of nitrogen or phosphorus*

Treatment	Conc. (p.p.m.) in original culture soln.		Mg. algae inoc. into 400 ml. soln. lacking		Mg. algae recovered after 12 days	Growth in soln. lacking N or P as % of inoculum
	N	P	N	P		
A	6.8	0.45	27.5	....	30.2	110
B	13.6	0.45	27.0	....	45.3	168
C	20.4	0.45	24.3	....	47.3	195
D	27.2	0.45	25.6	....	46.0	180
E	20.4	0.05	....	20.5	35.5	173
F	20.4	0.09	....	28.0	56.5	202
G	20.4	0.18	....	28.1	77.7	277
H	20.4	1.80	....	30.8	125.7	408

The results show that considerable growth took place in culture solutions lacking nitrogen or phosphorus, particularly from transfers with initially high levels of the element. The maximum in-

crease in growth in a solution lacking nitrogen was approximately 100 per cent (treatment C) and in solutions lacking phosphorus 300 per cent (treatment H).

Discussion

The results presented indicate that neither nitrogen nor phosphorus was a limiting factor for for the abundant growth of *Microcystis* in the lakes from which samples were taken. However, it appears that the supply of nitrogen is present in relatively less excess than is phosphorus. This finding is of interest in connection with proposals for controlling growth of algae in these lakes by removal of phosphorus from entering sewage effluents and industrial wastes. It would seem from the standpoints both of the high phosphorus content of the cells and the much lower supply of nitrogen in relation to need that such a procedure would be of doubtful effectiveness unless at the same time the phosphorus content of all inflow water and the residual phosphorus already present in the lakes could be brought to very low levels.

Since the percentage of nitrogen and phosphorus in *Microcystis* varied markedly in different growth stages, it is obvious that the analysis of the algae for only nitrogen or phosphorus, or probably any other single element, could not be used as an accurate index of supply of that element in lake waters. In fact, the reliability of the method would be improved if it were applied to additional elements so that variations in content between three or more separate elements could be used in estimating the adequacy of supply of each.

The considerable growth of *Microcystis* after transfer from media containing high concentrations of nitrogen or phosphorus to solutions lacking either one of these elements indicates that algae in a lake could begin growth in a nutrient-rich region, such as the layer next to the bottom muds, where they might absorb sufficient quantities of various elements to permit considerable growth after being carried into nutrient-deficient surface layers. Similar evidence for the utilization of excess quantities of essential elements by green algae and diatoms has been reported by Ketchum (1939) and Rodhe (1948). This utilization of stored nutrients illustrates one of the difficulties likely to be encountered in attempting to correlate growth of algae with the composition of the water in which they appear as blooms. It would appear, however, on the basis of the consistent results obtained with *Microcystis* and their agreement with past experience in estimating nutrient supplies to crop plants, that the method presented above may be satisfactory for evaluating the adequacy of supplies of nutrients to aquatic organisms.

Summary

A procedure has been presented for evaluating the adequacy of nitrogen and phosphorus supplies in lake waters for *Microcystis aeruginosa*.

First a quantitative study was made of the relationships between yield and total nitrogen and phosphorus contents of the organism grown in nutrient solutions containing quantities of the elements varying from highly deficient to excessive amounts. The cell content of either nitrogen or phosphorus was found to increase with external supply over a wide range. However, over a major portion of this range the amount of growth remained practically constant. Thus, above the minimum level required for maximum yield, the critical level which remains fairly constant, there was a large excess content representing luxury consumption. This excess content, although it does not influence growth, does quantitatively reflect the abundance of the external supply.

The nitrogen and phosphorus contents of *Microcystis* collected from lake blooms were compared with the range of contents in the algae grown in the laboratory. The results showed that both the nitrogen and phosphorus contents of the collected samples were in the range of luxury consumption and so far above the critical levels that neither element could be considered the limiting factor for algal growth in the lakes from which the samples were taken. However, nitrogen was present in relatively less excess than phosphorus.

The general application and limitations of the procedure as a means of determining the adequacy of supply of essential elements to aquatic organisms are discussed.

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CLIMATES OF THE GREAT SMOKY MOUNTAINS[1]

ROYAL E. SHANKS
Department of Botany, The University of Tennessee, Knoxville, Tennessee

Few areas of comparable size outside the tropics approach the Great Smoky Mountains of Tennessee and North Carolina in number of species which attain tree size. Most of the species in this remarkable list of about 125 reach their upper or lower climatic limits in the Great Smokies. This region thus provides a rare opportunity to study the behavior of a series of species at or near their climatic limits.

Such a study, initiated early in 1950, and supported in part by a Sigma Xi grant-in-aid, centered around a detailed comparison of the seasonal course of growth of seven tree species at five different altitudes, and required an investigation of the specific "habitat climates" in which the sample trees were growing. To provide a background against which the habitat data might be evaluated, it was necessary to analyze the official weather records of the Smoky Mountain Snowfall Study, a joint project of the Tennessee Valley Authority, National Park Service, and U. S. Weather Bureau, which ran from January 1946 through March 1951. The cooperation and assistance of these agencies and of the Society of the Sigma Xi are gratefully acknowledged.

The present report is concerned with the general pattern of mountain climates expressed in the records for 1946-50. Although the period of available record is relatively short, these five years differed enough among themselves that they are believed to constitute a good sample of the variability with respect to temperature, precipitation, and humidity.

Data from four of the weather stations have been used in the present study. These stations span the route along which the tree samples were selected and along which spot habitat data are available. Weather bureau type maximum and minimum thermometers and a Friez hygrothermograph were installed at each station, in a louvred, double-roofed shelter of U. S. Weather Bureau type. Precipitation gauges were equipped with Alter shields and precipitation measurements were made by weighing. The stations were serviced daily, and precipitation, maximum and minimum temperatures and a psychrometer reading were recorded. Tabulations of hourly values of temperature and relative humidity were prepared by T.V.A. personnel by adjusting hygrothermograph tracings to the daily temperature and humidity values. This procedure resulted in detailed records of unusual precision, which are on file with each of the cooperating agencies.

The locations of the stations are mapped by Smallshaw (1953) and in the T.V.A. precipitation reports. Those at the opposite ends of the series are about 11 miles apart. The station at Park Headquarters (1460 ft.) is on the landscaped lawn of the headquarters building, near the confluence of Fighting Creek with the West Prong of the Little Pigeon River, where it is in a position to receive cold air drainage from an extensive area on the northwestern flank of the Smokies. This valley flat is almost completely surrounded by low hills and ridges which restrict the horizon by as much as 16 to 18° to the east and northwest. Remnants of the natural vegetation indicate that the area was originally characterized by cove hardwoods with oak and pine on the drier sites. This forest included some low-altitude species which were not present at the higher station, such as sweet gum (*Liquidambar stryaciflua* L.), persimmon (*Diospyros virginiana* L.), blue beech (*Carpinus caroliniana* Walt.), hackberry (*Celtis laevigata* Willd.), red mulberry (*Morus rubra* L.), and winged elm (*Ulmus alata* Michx.).

The station at Alum Cave parking lot (3800 ft.) is in a valley with marked topographic protection. The horizon is restricted in all directions by 10 to 25° and the immediate location of the instrument shelter is slightly lower than the parking area and roadways, which completely surround it. The vegetation is a fairly open stand of yellow birch (*Betula lutea* Michx. f.) and hemlock (*Tsuga canadensis* (L.) Carr.) with a heavy understory of *Rhododendron maximum* L. The precipitation gauge was exposed with standard 45° clearance at the edge of the parking area, but the instrument shelter was shaded by trees for short periods during the day and the rhododendron thicket around it probably retarded air movement.

The station at Newfound Gap (5000 ft.) is on a small projecting spur on a steep (30°) northerly slope, near the edge of Newfound Gap, the saddle in the state-line ridge through which the highway passes. The gap was originally occupied by

[1] Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. 139.

beech (*Fagus grandifolia* Ehrh.), the adjacent slopes and ridges including the vicinity of the weather station largely by red spruce (*Picea rubens* Sarg.). To the south, the horizon is locally restricted by 30° by the ridge on whose north flank the weather station is situated.

The highest station in the series was at 6300 ft., on the southerly slope of Clingman's Dome, the highest mountain in the Great Smokies. It was in an exposed position at the edge of the Forney Ridge parking area, on a site formerly occupied by Fraser fir (*Abies fraseri* (Pursh) Poir.) with some mixture of red spruce. The present secondary vegetation around the area is a thicket dominated by fire cherry (*Prunus pensylvanica* L.f.), yellow birch, and blackberry (*Rubus canadensis* L.). The shelter and precipitation gauge were fully exposed to sun and wind, the only restriction of horizon being due to the ridge crest to the north (11°). The average slope below the station is south, at an angle of about 14°.

Precipitation

Both temperature and precipitation change markedly in the approximate mile of relief in the Great Smokies. The well-known coolness and raininess of the mountain climates are borne out by the data for the sample period of five years. The first graph (Fig. 1) summarizes the altitudinal variation in annual precipitation 1946-50, including data from an additional 2500 foot precipitation station. The precipitation records of the Smoky Mountain Snowfall Study have been analyzed in greater detail by Smallshaw (1953). The station at Park Headquarters is not much higher than nearby stations in the Appalachian Valley and does not show enough increase in precipitation over them to indicate a strong "approach effect" at the base of the mountain mass. Above this point, there is a rapid and regular altitudinal increase in precipitation to 5000 feet. The 6300 foot station holds the maximum record for the series, with over 105 inches in 1949, but does not average much higher than the 5000 foot station, a lack of difference attributed by T.V.A. analysts to difference in exposure of the station (Tennessee Valley Authority 1950, Smallshaw 1953).

In summary it might be said that the precipitation at the base of the mountains is not far different from that of the adjacent valley area, but that it increases sharply with altitude, and has increased by 50% by the time the lower limit of the spruce-fir zone is reached, at 4500 to 5000 feet.

Temperature

The temperature gradient is illustrated by a profile showing mean annual temperatures for the four stations for the five year period and by a series of profiles based on the mean monthly temperatures for the year 1949 (Fig. 2). Profiles for the first six months of 1950 are also presented for comparison.

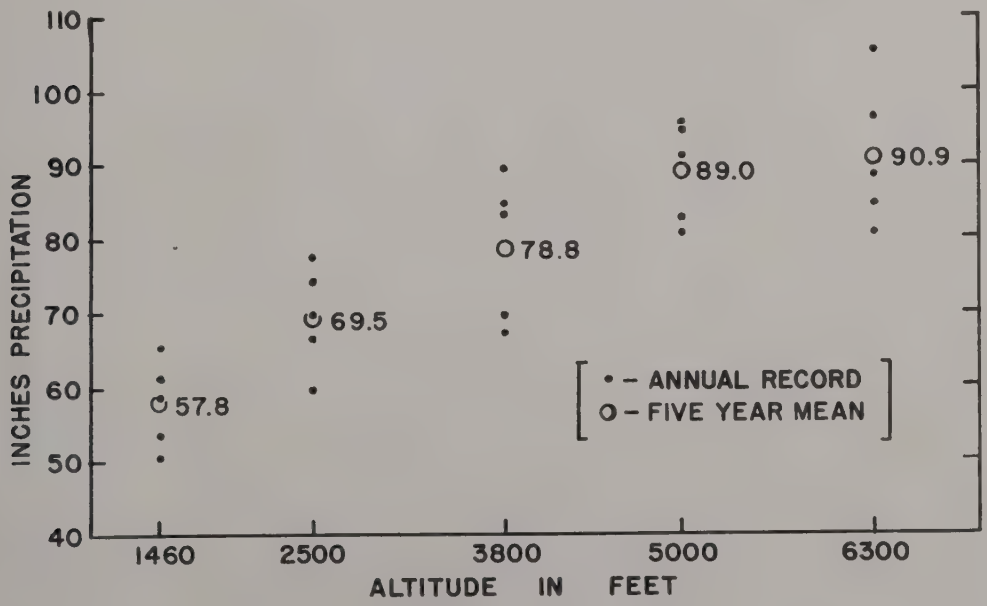

Fig. 1. Altitudinal variation in precipitation 1946-50.

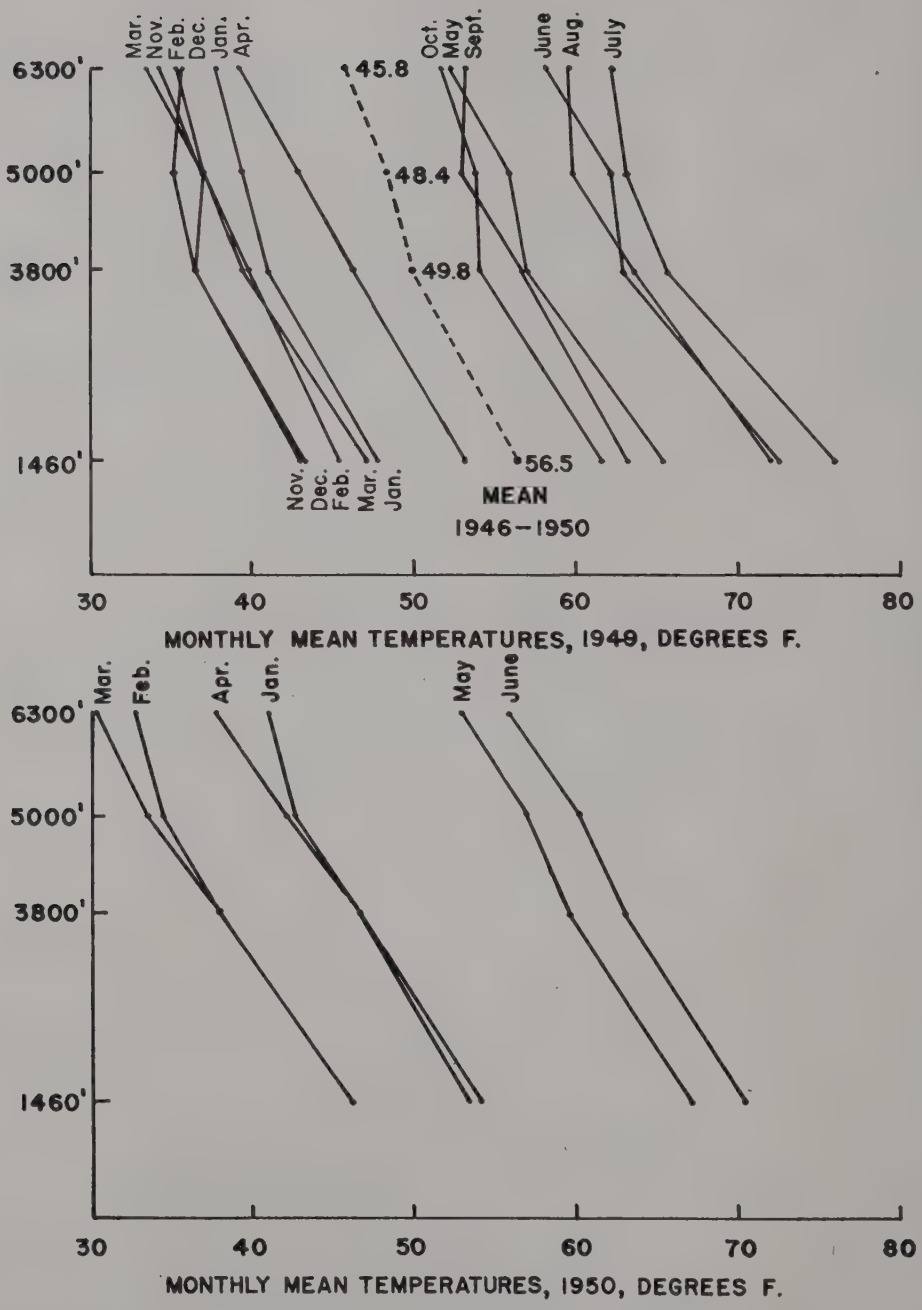

FIG. 2. Temperature profiles for the years 1949 and 1950.

The average rate of decrease with altitude is 2.23° F. per thousand feet in contrast with the 3.37° given by Peattie (1936) as the mean for 17 extra-tropical mountains, or Früh's figure of 3.07° based on 162 Swiss stations, the lowest figures cited by Peattie. While the high altitudes are thus not as cool as might have been predicted, the spruce-fir forests nevertheless average 10 to 15° F. cooler than the base of the mountains during their growing season.

The seasonal temperature trend is illustrated by the monthly profiles for 1949. Progressive cooling occurred from January through March, but by April spring had arrived at all but the uppermost station, which remained cold for another month. The lower and upper ends of the April and May profiles, respectively, suggest that it takes spring about a month to "climb the mountain."[2] The same relationship appears in the 1950 data. The 1949 data illustrate the marked contrast between the six warm months and the six cold months of the year and emphasize the rapid warming between April and May and the sharp cooling between October and November.

The 1950 profiles document the phenomenal January of that year which had about a dozen species of herbaceous plants in flower in the lower coves. January was actually as warm as April at all elevations, and as warm at Park Headquarters as May on Clingmans Dome. The extreme variability of the winter weather in this area is illustrated and its unpredictability is emphasized. The greater variability of winter months is also illustrated in Table I.

TABLE I. *Temperature summary, 1946-50, Park Headquarters, 1460 feet*

	Five-year mean	Highest monthly mean	Lowest monthly mean	Range of monthly means
January	43.3	54.0	31.8	22.2
February	41.7	45.7	30.8	14.9
March	47.2	54.6	37.3	17.3
April	56.8	59.6	53.0	6.6
May	66.0	69.4	63.9	5.5
June	70.7	72.4	69.0	3.4
July	73.6	76.6	69.5	7.1
August	71.6	74.2	69.0	5.2
September	66.3	70.4	63.2	7.2
October	57.7	61.5	52.8	8.7
November	45.4	50.0	40.2	9.8
December	39.4	43.4	32.9	10.5
Annual	56.5			

THORNTHWAITE 1931 CLIMATIC CLASSIFICATION

With the pattern data thus far summarized it becomes reasonable to ask the question "where is it possible to find a low altitude equivalent of our high mountain climate, if indeed such exists?" or the related question "to what degree does the Southern Appalachian spruce-fir climate correspond with the low altitude spruce-fir climate of the boreal forest?" This is an extension of the problem of the climate of the Appalachian spruce-fir forest considered by Oosting and Billings (1951), which is made possible by additional data now available. Thornthwaite's climatic systems (1931, 1941, 1948) have been selected for this analysis since they express both temperature and moisture indices in numerical terms and facilitate direct comparison. Although the two Thornthwaite systems differ in their bases and numerical values, they lead to similar conclusions in this case, and the following discussion is in terms of the older, more familiar system, illustrated in Figure 3. In its coordinate system, temperature increases from top to bottom and available moisture from left to right. The temperature (T-E) index is based on a summation of monthly values of the precipitation data. Points have been plotted for Memphis, Knoxville, and Johnson City, Tennessee, and the four stations in the Great Smoky Mountains National Park as well as for the Acadian Section of the Canadian forest, the nearest equivalent to our high mountain climate discovered in the literature (Halliday 1937). Index values used in plotting are listed in Table II, which also gives values according to the later system for each of the mountain stations.

Several points in Figure 3 deserve special notice: (1) the altitudinal increase in effective

TABLE II. *Index values used in plotting positions of stations in Figures 3 and 4, with climatic provinces indicated*

Station	Thornthwaite 1931 system			Thornthwaite 1948 system		
	P-E Index	T-E Index	Climatic Province	Moisture Index	TE Index	Climatic Province
Great Smoky Mts.						
1460 feet	121.0	74.0	$B_8rB'_b$	91.2	29.85	$B_4rB'_{2a'}$
3800 feet	208.4	53.7	ArC'b	200.5	24.37	$ArB'_{1a'}$
5000 feet	241.6	49.4	ArC'b	242.0	23.44	$ArB'_{1a'}$
6300 feet	274.1	40.4	A+rC'b	285.1	20.88	$ArC'_{2b'_4}$
Tennessee						
Memphis	84.7	86.3	B_6B'	45.9		
Knoxville	92.0	78.0	B_6B'	55.0		
Johnson City	105.4	75.2	B_7B'	71.8		
Acadian Forest						
Miramichi	131.8	36.8	ArC'c	104.8*		ArC'_2
Central	132.4	37.6	ArC'c	105.5*		ArC'_2
Atlantic Slope	165.0	37.3	ArC'c	146.0*		ArC'_2
Cape Breton Plains	172.1	37.9	ArC'c	155.0*		ArC'_2

*Computed from Halliday's data with Thornthwaite's formula: $.8I_m+48=$P-E index of earlier system.

[2] Unpublished phenological records of Arthur Stupka, Park Naturalist, G. S. M. N. P., indicate that it takes consistently more than a month—"possibly six or eight weeks."

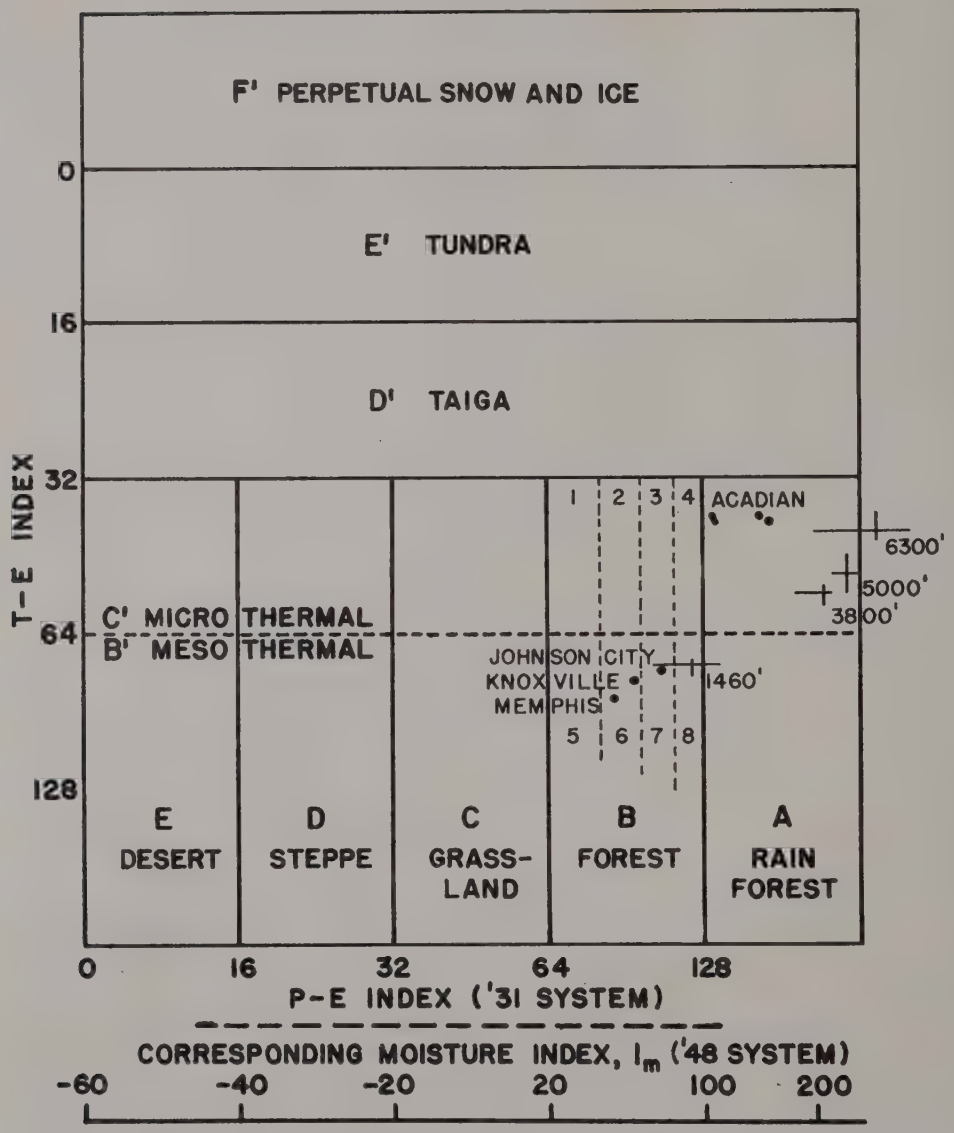

FIG. 3. Graph showing position of the mountain stations in relation to other selected stations according to the older Thornthwaite system. Bars show ranges of values for the 1946-50 period; they cross at their means.

moisture and decrease in temperature are accordant; (2) the 1460 foot station represents, in this five-year period, the B_8B' combination which was not believed to exist in eastern U. S. at the time of Thornthwaite's 1941 publication; (3) major boundaries of both temperature and moisture according to the Thornthwaite 1931 system are apparently crossed a short distance above the 1460 foot station; and (4) the spruce-fir forest climates of the Great Smoky Mountains fall near or outside the super-humid edge of the graph about half way between the taiga boundary and the micro-mesothermal boundary; they might be characterized as cool-temperate (microthermal) rain forest climates.

The design of Thornthwaite's graph implies by its horizontal and vertical lines that in cold climates temperature is likely to be limiting, in warm

climates moisture. The present data call attention, however, to that part of the warm range where moisture is not limiting, specifically, the "rain forest." Here vegetational boundaries would likewise fall along horizontal lines—the equivalent of altitudinal limits in our super-humid mountains.

The present data suggest that Thornthwaite's (1941) B_4 subprovince, designated *spruce-fir,* should be interpreted as meaning that any point from there to the right in Figure 3 may support spruce-fir forest. For the Great Smoky Mountains it appears that the microthermal spruce-fir climate is further restricted by a T-E boundary of approximately 50 along the lower edge.

Thornthwaite 1948 Climatic Classification

Application of Thornthwaite's later system (1948) to these data shows similar altitudinal gradients of moisture index and thermal efficiency index to those of the earlier system. The accordant gradient relationship is illustrated in Figure 4, which represents the position of each station by a point on a coordinate graph, using data from Table II. Although the numerical values differ, the boundaries between moisture provinces are the same as those shown in Figure 3, the humid-perhumid boundary falling a short distance above the 1460 foot station. However, as pointed out by Thornthwaite (1948), the thermal efficiency provinces of the newer system differ from those of the former system both in their basis and in the geographic span of stations included, although the symbols and descriptive terms are generally the same. Mesothermal climates are more extensive in the newer system. Thus the mesothermal-microthermal boundary falls just above the 5000 foot station according to the newer system, rather than between 1460 and 3800 feet, and approximates the most critical bioclimatic boundary in this mountain area, the lower limit of continuous spruce-fir forest with its characteristic biota.

The newer system also provides a means of direct comparison of precipitation and potential

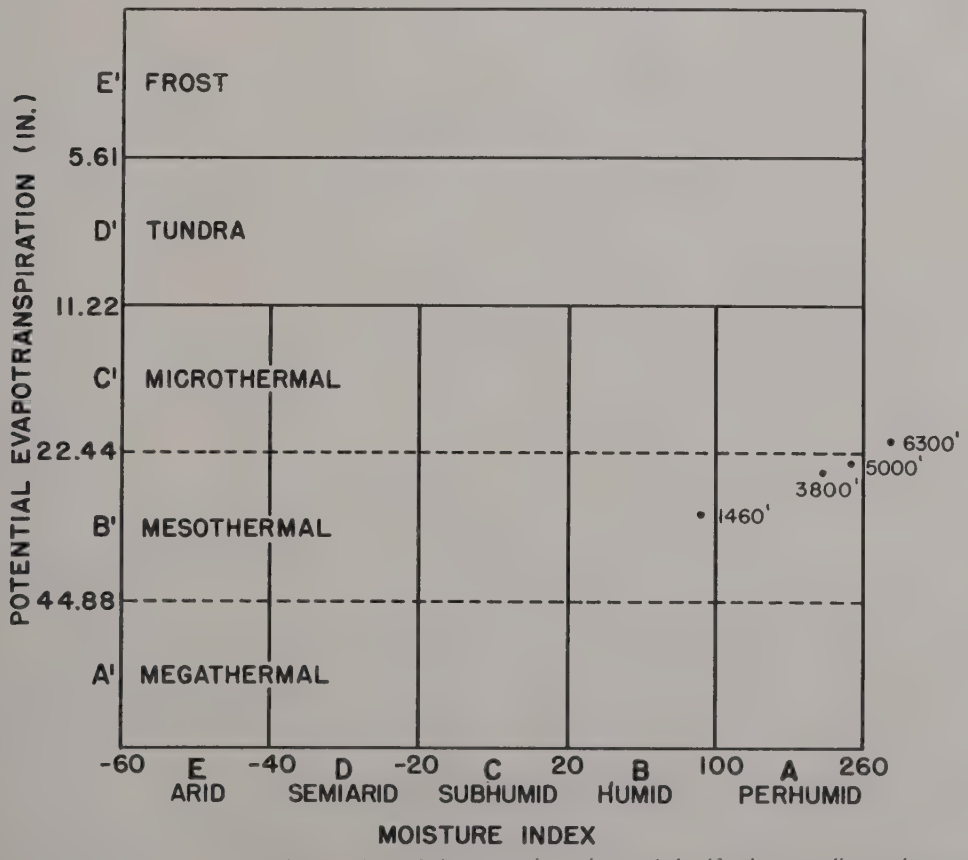

Fig. 4. Graph showing relative positions of the mountain stations and classification according to the newer Thornthwaite system.

evapotranspiration, and of graphic portrayal of the relationship (Fig. 5). The marked increase in precipitation with altitude is attended by an even greater increase in water surplus, since potential evapotranspiration decreases with altitude. The curves are somewhat erratic due to the short period of record, but the general seasonal trend and altitudinal relationship appear to be representative. In only one case, September at 1460 feet, does a monthly value of potential evapotranspiration exceed the precipitation, and then only by .49 inches. The fall "fire season" regarded as a regional climatic characteristic is suggested by the decrease in moisture surplus in the months of September and October at all altitudes.

Conclusion

It seems that the answer to the question of altitude-latitude equivalence, in terms of the Thornthwaite climatic systems, must run something like this: the taiga spruce-fir forests are, in general, both colder and drier than the spruce-fir of the Southern Appalachians. Only in northern New England and the adjacent Maritime Provinces of Canada and in the coastal region of Washington and Oregon is the cool super-humid climate of the Southern Appalachians approached near sea level. Perhaps the nearest low-altitude equivalent in terms of both climate and vegetation occurs somewhere in northeastern Maine or adjacent New Brunswick, about 1000 miles to the northeast.

Summary

Analyses of weather records for the northwestern slope of the Great Smoky Mountains for the period 1946-50 lead to the following conclusions:

(1) a gradual decrease in temperature occurs from the base of the mountains upward, with the spruce-fir zone above 5000 feet averaging 10 to 15°F. lower than the base of the mountains during the growing season;

(2) a gradual increase in precipitation occurs from the base of the mountains upward, this increase amounting to 50 per cent by the time the spruce-fir zone is reached; the five-year average in the spruce-fir zone is over 90 inches, and the long-time average must be well over 80 inches;

(3) either of the Thornthwaite systems of climatic classification is adequate to differentiate the climates of the stations at different altitudes; major boundaries of both thermal efficiency and effective moisture are crossed in the series of stations according to either system; however, the mesothermal-microthermal boundary of the newer system approximates a more critical bioclimatic boundary than that of the older system;

(4) the mountain climates above an altitude of 2000-2500 feet are extremely humid, falling into the *rain forest* or *perhumid* class; at spruce-fir altitudes they fall near or outside the super-humid edge of the Thornthwaite (1931) graph, exceeding the highest moisture values reported for comparable forests;

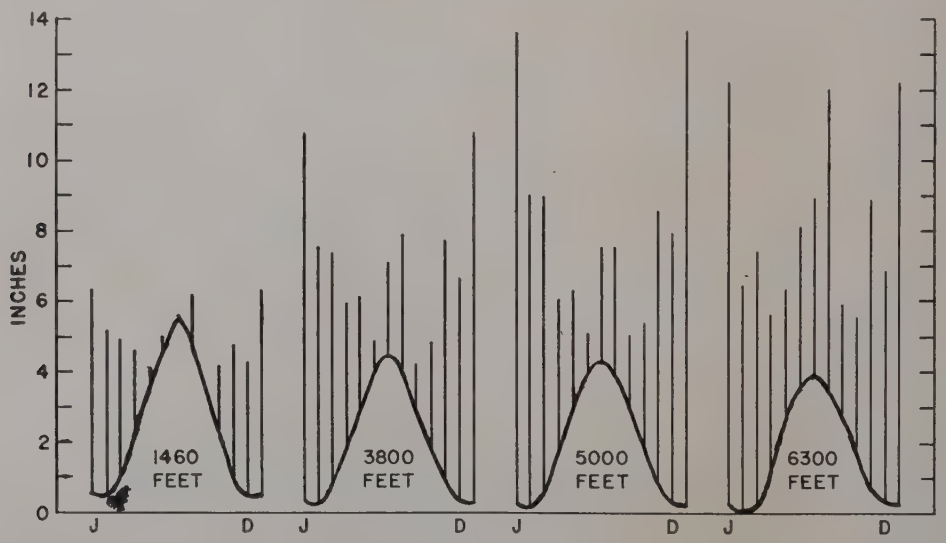

Fig. 5. March of precipitation and potential evapotranspiration 1946-50. The curves connect the monthly values of potential evapotranspiration; the bars connect these points with those representing precipitation and thus indicate magnitude of water surplus.

(5) these recent data indicate a need for revision of the Southern Appalachian portion of Thornthwaite's (1948) maps of Moisture Regions in the U. S. and Average Annual Thermal Efficiency, calling for a moisture sequence up to *perhumid* (A) and a thermal efficiency sequence up to *microthermal* (C'_2) in the Great Smoky Mountains in addition to those already shown in the Blue Ridge and the mountains of northwestern North Carolina.

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EQUATIONS DESCRIPTIVE OF FISH SCHOOLS AND OTHER ANIMAL AGGREGATIONS

C. M. Breder, Jr.
The American Museum of Natural History

Introduction

In an effort to understand better the basic nature of the influences at work in a school of fishes as well as in other less compact aggregations, Breder (1951) discussed, in passing, the possibility of applying physical equations to such groups, without going into the matter further. The present comments are a continuation of those thoughts including an alegbraic approach to the forces which maintain the integrity of fish schools. The purely theoretical considerations which are here presented have been applied to data obtained from real fish schools of various species with results which are given in the later portions of the paper.

Much of the field work which led to these studies was carried out at the Lerner Marine Laboratory on Bimini in the Bahamas. The author is grateful to Dr. L. B. Slobodkin for reading the manuscript and for his exceedingly helpful and constructive criticism.

Basic Considerations

A typical fish school shows clear evidence of both attraction and repulsion between the individual fishes. In such a group, the operation of these two contrary influences may be readily seen in its simplest form where separated fishes rush together to a certain specified distance beyond which their refusal to move any closer is absolute. This behavior results in the formation of the fish school proper, where all members of the group stay spaced a standard distance apart, within very narrow limits. This feature of the fish school has been the subject of comment by various students, including Parr (1927), Breder (1929), Breder and Nigrelli (1935), Bowen (1931, 1932), Spooner (1931), Shlaifer (1942), and Breder and Halpern (1946).

If we accept the proposition that there is an attraction between fish and fish which varies with the distance between them and that there is also a repulsion which varies with this distance, the observed behavior of a school of fishes becomes suggestive of the nature of these two unknowns. The repulsion is evidently more effective at short distances than the attraction for otherwise the fish would approach to contact. Likewise at greater distances the attraction must be larger than the repulsion or they would not band together at all. It should be borne in mind that these two forces are not necessarily mediated by the same sensory mechanism. While the attraction of fish to fish has been shown to operate by means of vision, or at least, disappears with the loss of sight, the repulsion may work on a rather different basis. Operating at short distances, in addition to the visual component, other clues could include water movement, sound, odor and taste. Such normally schooling fishes, when experimentally separated, will swim toward one another as soon as visual contact is established. So far as simple observations can determine it would appear that they accelerate ever so slowly as they

approach. This could be determined only with certainty by some experimental, perhaps cinematographic procedure. When they reach a certain distance apart they approach each other no closer and hold what is apparently the point of equilibrium between attraction and repulsion. Evidently the repulsion overcomes the attraction at that point.

Since the repulsion must be greater than the attraction at very short distances between the fishes and the attraction greater than the repulsion at large distances, the two forces must be equal at the distance between the fishes normally found. This situation may be expressed as follows. Letting a = the attractive force, r = the repelling force, d = the distance between the fishes and c = a measure of the cohesiveness of the group (the sum of a and r) then the following conditions obtain: when d = the normal distance observed between fishes in a school, $a - r = 0$; when $d >$ the normal observed distance, $a - r > 0$; and when $d <$ the normal observed distance, $a - r < 0$.

Consequently whatever values are assigned to a and to r the latter must be subtracted from the former so that c will be negative when d is small and positive when d is large. This may be accomplished by the development of mathematically suitable exponents of d. The resulting value of these two opposite forces may be considered as an index of the cohesiveness of the group of fishes, expressed where n and m are exponents which may be equal or unequal

$$c = a/d^m - r/d^n \qquad (1)$$

Considering only the modification of r, if the repulsion is taken to vary inversely as the square of the distance, as in Coulomb's law of magnetism and electrostatics then the equation may be written

$$c = a/d^m - r/d^2 \qquad (2)$$

If a varied in the same manner as r, that is $m = n$, no appropriate equation could be developed, but if a very small value is assigned to the exponent m an equation which does express the conditions can be developed, for instance as follows

$$c = a/d^{0.005} - r/d^2 \qquad (3)$$

Since to describe the conditions found, the exponent of d for the attractive influence must be very small, it may for present purposes be reduced to 0. Thus any value for d becomes 1 and the equation simplifies to

$$c = a - r/d^2 \qquad (4)$$

Actually that such a condition develops is not surprising for as already noted the attraction is absent without vision. The problem then becomes one of the difference in attractive force of say a fish 2 feet or 4 feet away. It could very well be that the smaller the retinal image of the other fish the greater the urge to enlarge it, which results as the fish approach each other. This is actually a basic point in the primary analysis of school formation by Parr (1927). This would, of course, reduce the exponent m to be 0. With this value, a/d^0, or simply a, as in equation (4), values for the whole expression may be calculated. Obviously r involves two objects such as two fish or two schools as in Coulomb's law previously noted or Newton's law of universal gravitation and similarly may be developed as r_1 and r_2 bringing the equation to the following form.

$$c = 1 - r_1 r_2/d^2 \qquad (5)$$

With r_1 made equal to r_2 and d made equal to r_1 the value of c becomes 0. Then the relationship between c and d for all other values of the latter may be calculated with the values of r_1 and r_2 held constant. A curve plotted from such a procedure, with $r_1 = 3$ is shown in Figure 1. This purely hypothetical curve has several interesting characteristics in connection with present considerations. In its positive range it becomes virtually a horizontal line showing that attraction between fish and fish quickly reaches a value which shows little further change with greater distance (to the limit of visibility ?). The point of neutrality, where attraction equals repulsion, represents the distance which the fishes in a school maintain between each other. Below the point of neutrality the curve becomes abruptly and strongly negative. The negative portion approaches zero on d and the positive portion approaches 1 on c, both as asymptotes.

It should be borne in mind that the above comparison of the social behavior of schooling fishes with the forces displayed by inanimate objects is made with the full recognition that they are entirely distinct. That is, the notation describes the observed schooling without postulating the precise nature of the attractive forces.

The values for r may be further analyzed so that r_1 and $r_2 = f_1 p_1$ and $f_2 p_2$ where f = number of fish and p = potential influence of one fish. For present purposes, f may be taken as equal to 1, which in effect is the influence of two fish on each other, a "school" of two fish. This may be used in consideration of the internal structure of a school while larger values of f would be invoked in considering the influence of one school on another. If the fish are equipotential, within very narrow limits, which they evidently are in a closely knit school, p may be made to equal 1, or any other value provided it is the same for each fish. The case of small fish "schooling" with large ones, such as the instance of pilot fish and sharks, will be taken up later.

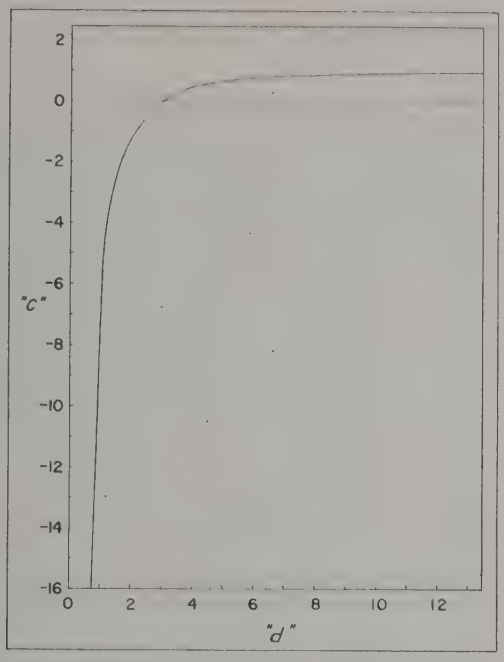

FIG. 1. Graph of the equation $c = a - r_1 r_2 / d^2$ where r_1 and r_2 each = 3.

The full equation may be given the following expression:

$$c = 1 - (f_1 p_1)(f_2 p_2)/d^2 \qquad (6)$$

Since all fish schools studied have been shown to operate on a visual basis, the preceding could only apply to situations involving a few individuals, strictly only two. A list of the species studied is given by Breder (1951). The fact that some fishes may be hidden behind others should not have any important effect until large groups are considered. Since the mechanism of attraction between visually motivated fishes differs from the mechanism of attraction accounting for gravitational and magnetic phenomena it is obvious that corresponding differences in the schooling equation must appear if it is to include reactions between large groups of fishes where only a small part of the total number of individuals is visible to any one fish. This then must be considered a surface effect rather than an effect of mass. Surface as used here actually may be a band of about six rows of fishes deep. In various cases it may take that many to fully block out those behind them. These hidden fishes may extend only a few more rows or many thousands and be without effect because they are completely out of sight.

Considering a fish school as a geometrical solid of uniform density, it is possible to handle the problem by recourse to certain considerations involving the properties of space. Since the surfaces of similar figures vary as the squares of corresponding linear dimensions while the volumes vary as the cubes, it is possible to calculate the influence of any similar school if certain characteristics be known. As only part of the total "surface" would be visible to an exterior fish or another school, only that amount of surface would be influential. If a school be imagined as a perfect sphere, it would follow that its influence would not be proportional to its volume, nor to its surface, but would be proportional to the area of a circle of the same diameter, which is, of course, the visual image of the sphere. This would reduce the school to its lowest external influence since a sphere has the minimum surface possible in relation to volume. It also is not the characteristic shape of fish schools, which are more likely to be flattened structures in which the difference between the value of the surface and volume is much less. If a second model school is taken to be in the proportion of 1 unit long, 1 unit wide, and 0.1 unit deep, a condition approximating that form which many schools take frequently, the numerical value of the area of any one edge, *i.e.* 1 x 0.1, is the same as that of the volume, or the two increase equally. If a third model be given the proportion of 1 unit long, 0.1 unit wide and 0.1 unit deep, another approximation to the shape of many fish schools, it should have ten times as much influence when viewed from either side than when viewed from either end. This model has its surface-volume relationship about midway between the sphere and square model, when viewed side-on, and much less than the sphere, when viewed end on. This is clear when it is remembered that we are not dealing with the total surface of these figures but just the visible area from a given viewpoint. If the second model, 1 x 1 x 0.1, be viewed side-on naturally the area viewed increases at a much faster pace than the volume. Since most schools are apt to be more or less circular, elliptical, or drawn out and not very deep it follows that the ratio of the area to volume will be mostly between 1 to 10 and 1 to 1 when viewed from the most influential aspect.

These considerations have bearing on the equation in the sense that the value assigned to f of equation (6) refers to the number of fish visible to an individual and not to the total number in a school. This condition obtains both for a fish deep in a school or one viewing a school from some external point. From this it follows that if the area shown by a school from a given viewpoint could be obtained, its influence should be proportional to f of the equation.

If it is eventually shown that certain or all fishes are able to school effectively by other than visual cues, the preceding considerations would have to be appropriately modified toward that of the involvement of the effect of the mass of a school rather than the case of the effect of the surface of a school as above discussed. However, the observed breaking up of schools in the absence of light indicates that these other sensory influences must, at best, play a very minor role in the maintenance of a school in the sense here used, although it is conceivable that other senses are involved in keeping fishes from wandering completely out of range of each other.

Comparison with Real Fish Schools

In order to test the validity of the preceding theoretical considerations, recourse was made to actual fish schools to obtain empirical data. Perhaps the simplest method is to examine photographs of schooling fish which have been made from directly above, as are some shown by Breder (1951). Figure 2 illustrates the appearance of typical fish schools. This is shown here for the benefit of readers who may not be familiar with the remarkable regularity of the true fish school as distinct from a simple aggregation. Such pictures, of course, may be either single still photographs or successive frames of motion picture studies. Both have been used for obtaining the data considered in this section of the study. Since here we are not dealing with mathematical models but with actual physical and biological imperfection, it is found that we must employ mean values and ranges as is done in the following illustrative cases. In Table I, data are given for four schooling types. The heading d_1/l is used as the photographs are not directly measurable in absolute units. The distance between individual fishes, d_1, is thus expressed as a decimal part of the mean length of the fishes measured where $l =$ the length of the fish. The numbers in parentheses indicate the number of pairs measured. In the two cases where twenty pairs were measured no statistical difference could be found between all taken together and either half. This is a measure of the consistency of these schools and is adequate for the present purposes of illustration. For any problem which might be based on this system of annotation larger numbers would, of course, be desirable. The known mean lengths of the fishes in mm. were used to calculate the maximum and minimum lengths of the individuals measured in arbitrary units on the photographs. In each case the closest pair and most distant pair found in the photographs was included. In each aligned pair the mean of the lengths of the two fishes was taken. The distance between was measured at the widest part of the body of parallel swimming fishes.

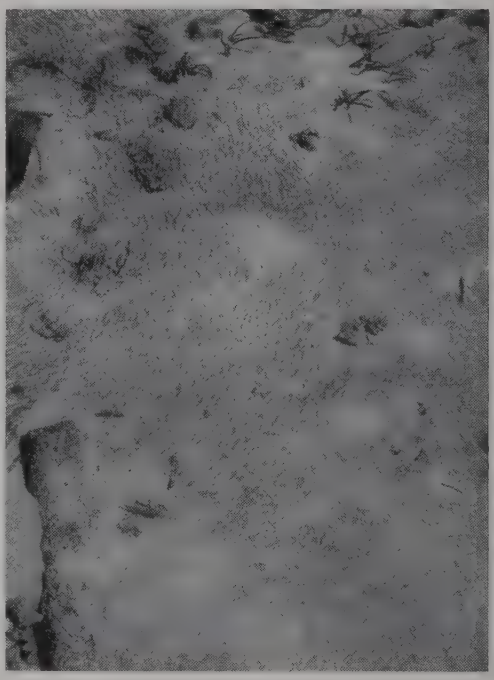

Fig. 2. An advancing school of *Jenkinsia* as seen in shallow water on a calm day. This is only about one-tenth of the entire school, which widens out beyond the limits of the photograph.

The data in Table I at once show certain differences between the species. The column d_1/l shows that the individuals in a school of *Sardinella* approach each other closer in proportion to their lengths than do the others. *Jenkinsia* forms the loosest schools, with *Atherina* next to *Sardinella* and juvenile *Ameiurus* in third position. These relationships agree with general observation on these four species. The standard error column gives a ready measure of the "accuracy" of the arrayed ranks of fishes. That is, the more "systematically" the fishes deploy themselves the smaller will be the standard error, reaching zero if absolute perfection reigns. Here the little catfish outdo all the others with *Sardinella* second, *Atherina* third, and *Jenkinsia* least regular. In absolute size these four species range from the largest, *Sardinella, Jenkinsia, Atherina,* to *Ameiurus.* Thus the above discussed differences between the schools would appear to be specific behavioral matters rather than something associated with absolute size. In comparing physically similar

fishes of various sizes or the same species at different sizes it would be expected that Froude's law would become involved in these considerations. This law, which states that velocity varies as the square root of the length, $v \propto \sqrt{l}$, is used widely in engineering studies between vehicles which differ only in size. It applies equally to other motile objects, such as fishes when *similar types* are concerned. The reason for mentioning this law in present connections is that the velocity at which the various fishes are moving, in both relative and absolute terms, affects the distances which the individuals in a school must maintain between each other. A study of its relationship to present matters must wait on the obtaining of data on similar forms over a sufficient size range.

The expression $d_1/l = d$ of the numbered equations. With this value for d, points for the four curves may be calculated and the characteristics of these schools may be expressed graphically as shown in Figure 3. Note in this figure how strong the force of attraction is when the fishes reach as little as "one fish length" apart. Under usual conditions they scarcely ever reach as much as 40% of their lengths apart, which is less than twice the mean distance of the loosest schooler of the four, *Jenkinsia*. The insert in Figure 3 helps display certain of these features a little more clearly by plotting the distance between the different species in reference to these features. Here the mean of each is indicated by a dark spot and the standard error of d is indicated by a short cross line both positive and negative.

By varying the relative values of r in equation (3) over wider ranges, a very interesting family of curves may be developed, many of which, and perhaps all, within very wide limits, could be used to describe various forms of animal aggregation. If the value of a is reduced to near 0, positive values of c appear only with very great values of d, which is to say that such animals would be attracted at distances at which they could not see each other. In other words these would be solitary fishes, whose equation would have to change the values of a temporarily for reproduction at least. Negative values for r_1r_2 which could be either $r_1 - r_2$ or $r_1r_2(-1)$ give mirror image curves all values of which are positive and which approach $d = 0$ and $c = 1$ asymptotically. Probably such a case has no biological representation unless during the spawning of such species as goldfish it could be considered that the values change temporarily as the intimate contact of the spawning act is reached. This, of course, implies as the graph indicates that the closer the bodies are, the more they attract each other.

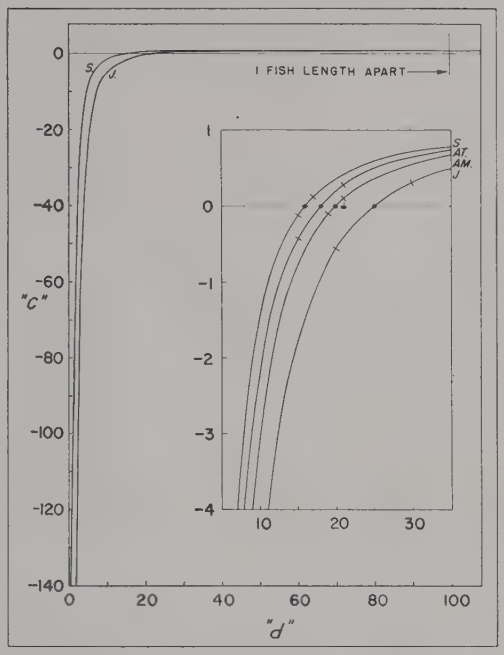

FIG. 3. Graph of the schooling behavior of four species of fishes; S = *Sardinella macropthalmia* (Ranzani), J = *Jenkinsia lamprotaenia* (Gosse), Am = *Ameiurus nebulosus* (LeSueur), At = *Atherina stipes* (Muller and Troschel). Only the highest and lowest are plotted in the main graph. The inset, which gives the significant part of the curve in enlarged form, also has the vertical index magnified by ten so as to more clearly separate the four species. The mean position of each is indicated by a dark spot and the standard error, both positive and negative, is indicated by a short cross line.

Very small positive values for a probably represent no fishes but may find expression in various colonial invertebrates or huddling mammals or birds that actually come in contact in their aggregating behavior.

The spread and deployment of some of these curves has other interests as well. Some cross the 0 value of c at much steeper angles than others. For example in Figure 4 the curve of $r = 1$ crosses at about 50° while that of $r = 25$ crosses at about 5°. Those of Figure 3 cross between about 40° to 50° which is characteristic of fishes which normally keep a distance considerably less than their own length apart. One would expect a type of aggregation represented by a curve which has a considerable portion approaching parallelism with $c = 0$ to be irregular and with a greater standard error. Individuals in a group represented by such a curve would not be hesitant to leave each other for greater distances, as for example, an aggregation of goldfish.

Other changes in the numerical values assigned

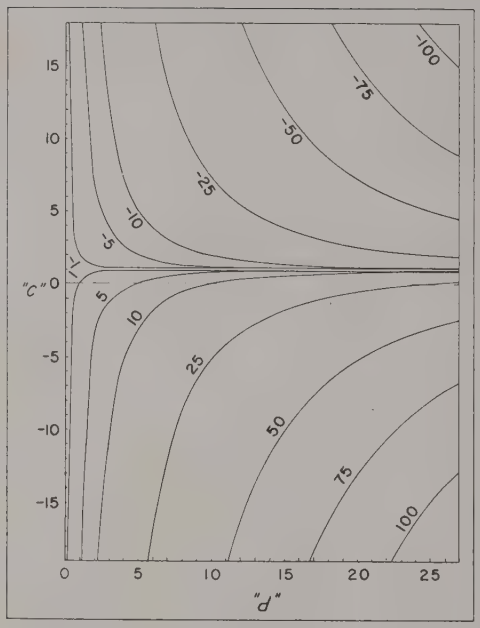

FIG. 4. The family of curves which the equation $c = a - r_1 r_2 / d^2$. Various examples with both positive and negative values for $r_1 r_2$ are indicated. The figures on the curves represent the values of r_1.

various quantities in the equation follow. Increasing a to more than 1 does not change the shape of the curve but raises it along the c axis, while decreasing it to positive values less than 1 lowers it. Making r_1 and r_2 unequal does not change the nature of these curves, for the curve marked $r_1 = 5$, for example in Figure 4, can equally well represent the condition where $r_1 = 5$ and $r_2 = 5$ or where $r_1 = 0.5$ and $r_2 = 50$.

Except in the last remark above, in the hypothetical and real cases so far considered the potentials of the individuals were equal, that is $a = b$. The case of a small jack "schooling" with the dorsal fin of a large shark, or pilot fish about the head of a shark, would call for $r_1 \neq r^2$. Very little study has been made of the attractive values of such unequal groups but Oshima (1950) performed some experiments with schools of large and small individuals of the marine catfish *Plotosus anguillaris* (Bloch) which are very suggestive in the present considerations. He found that when two schools of unlike sizes merged the fate of the joint group depended on the ratio of the mean lengths of the two groups. When below 0.65 they separated, but when above that value they remained united. In the case of such a separation the smaller group leaves the larger. The number of individuals of the smaller size-group likewise has an effect, the larger the number of small individuals relative to the larger, the longer the mixed group resists separation. Without laboring the point, these items would seem to fit nicely with the purely abstract considerations from which the present discussion has been developed. It is interesting to note that the natural schools of *Jenkinsia* which Breder (1951) studied showed the lengths to be in a ratio of small to large of 0.61 while the work of Schaefer (1948) on *Neothunnus* showed variation similarly from 0.73 to 0.50 in different schools, evidently as nearly as can be determined from their data, with a mean near 0.61.

TABLE I. *Data from dorsal photographs of fish schools*

Species	d_1/l	S. E.	Total length in mm.		
			Max.	Mean	Min.
Sarainella macropthalia (10)....	0.16−	0.014	160	150	140
Jenkinsia lamprotaenia (20)....	0.25+	0.055	66	58	50
Ameiurus nebulosus (20)....	0.20−	0.013	21	18	12
Atherina stipes (10)....	0.18+	0.031	60	51	45

The numbers in parenthesis following the fish names represent the numbers of pairs of fish measured. The known mean length of the fishes in the school in mm. was used to calculate the maximum and minimum lengths of the individuals measured in arbitrary units on the photographs. d_1/l refers the mean length of the fishes to unity and the distance between them as a decimal part of that length.

Working with the aggregating medaka, *Oryzias latipes* (Temminck and Schlegel), Nakamura (1952) more clearly showed the differences in the influences of groups of various sizes. He suitably arranged a device so that a single fish could view two chambers at opposite sides of its container. In these he placed various numbers of other individuals and at definite intervals noted which side of the container the single fish occupied. The data of his Tables 4, 5 and 6, rearranged and recalculated in a form more suitable for present purposes, are given in Table II. The first part of this tabulation shows clearly that the solitary fish was found to be located in the half of its container nearest the other fishes in direct proportion to their numbers. This is clearly indicated in the upper curve of Figure 5. Nakamura found that these data, with the frequency plotted against the logarithm of the number in the group, could be expressed by the equation $R = 9.89 \log S - 42.34$ where R equals the frequency and S the number of fishes in the group, up to a group of 32 fishes. The slope of a straight line in such semi-log treatment, from 32 to 128 fishes, is nearly 90° to the axis. In the second part of the experiment where the "b" chamber contained half as many fish as the other chamber, at no time was there a bias to the larger group over 65%. This value appeared only where two fish were opposed

to one. As their total numbers increased it is not surprising that the values approached 50%, as is shown in Figure 5. Also that this curve is more irregular than the first should be expected.

TABLE II. *Data on the behavior of a solitary* Oryzias *within sight of a homotypic group of different sizes*

No. of fishes in group	Percent of time test fish spent in half of container next to group of fishes	
	With no fish in opposite chamber	With one-half the number in group in opposed chamber
1.....	70+	..
2.....	76−	65
4.....	81−	61+
8.....	85	61+
16.....	90	62+
32.....	96−	44−
64.....	95	51
128.....	95	49−

Note. Each value represents the mean of 240 observations. Recalculated for present purposes from data presented in Tables 4, 5, and 6 of Nakamura (1952).

Values obtained from the above data by the equation $c = (f_1p_1)\ (f_2p_2)/t^2$

1.....	2.02	....
2.....	3.49	4.73
4.....	6.12	10.66
8.....	11.07	21.32
16.....	19.75	41.52
32.....	34.85	167.18
64.....	70.91	247.71
128.....	141.83	520.71

Calculated values for c and the differences from their observed values in the equations

	$c=1.110f$	$c_o - c_c$	$c=0.039f^{1.165}$	$c_o - c_c$
1.....	1.11	+0.91	....	.....
2.....	2.22	+1.27	4.57	+ 0.14
4.....	4.44	−1.68	10.24	+ 0.42
8.....	8.88	+2.19	22.97	− 1.65
16.....	17.76	+1.99	51.53	−10.01
32.....	35.52	−0.67	115.52	+51.66
64.....	71.04	−0.13	259.02	−11.32
128.....	142.08	−0.25	580.91	−60.20

The fact that the first curve reaches toward a value close to 100% as an asymptote should likewise be expected for if it were not for the partition of the apparatus, the solitary fish would, no doubt, have moved in with the group.

The fact that both these curves become substantially horizontal lines when fifty fishes are present has a very definite physical bearing on the equation presented in this paper. It must be borne in mind that, as developed, the equation was based on a "school" of two fishes and individual "pairs" were used in establishing curves for the four species studied. In any large group a certain amount of masking or shadowing of the influence of one fish by another would clearly reduce the essential potency of a group of fishes beyond a certain size because of the volume to the surface relationship, considering the group as a single unit. This suggests that the equation herein developed, while evidently sound for small schools and as a measure of the cohesiveness of any group, if it is to be extended to measure the influences of various large sized groups of fishes on each other, will have to be modified to take into account the masking effect that large groups exercise on their members.

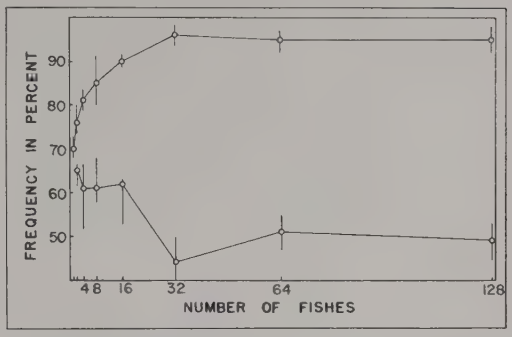

FIG. 5. Graph based on the data of Table II of the behavior of *Oryzias* under certain experimental conditions. Upper curve: Frequency of approach of a single individual to groups of various sizes with no competition. Lower curve: Same behavior but between competing groups one-half the size of the other. Vertical lines indicate extremes of the range between four experiments for each point. Based on the data of Nakamura (1952).

By handling the data on *Oryzias* in terms of the concepts previously discussed, a rather different use may be made of them. The equations (1) through (6) may be changed around so that the positions of a and r are exchanged without in any way modifying the resulting curves' mathematical characteristics. It is merely a question of which of these two antagonistic influences is considered as varying with square of the distance and which varying with a much smaller value. Since, in connection with these experiments, the experimental fish is mechanically prevented from getting into the range where r is effective only the influence of a need be considered. It is more convenient to use a notation eliminating the condition over which the fish have no voluntary control, expressed by the following

$$c = (f_1p_1)(f_2p_2)/t^2 \qquad (7)$$

Here f_1 = the single fish under test, f_2 = number of fishes in observed group and t = the decimal part of the time spent by the fish near the test group. With this change in the equation f and p refer to attraction as in (7), while in (6) these letters referred to repulsion. The values of p are taken as 1, for the fish are clearly equipotential, a point well established in the preliminary work dis-

cussed by Nakamura (1952). The final values of c here are in terms of time and not of distance. The data and calculated values are given in Table II and graphically in Figure 6. It might be expected on general considerations that these would be exponentials of the $y = kx^n$ type. They are very close to straight lines. Thus evidently the apparent straight line is a limiting form with $n = 1$. Fitting data to the first one the following equation is found:

$$y = 0.309\, x^{1.165} \qquad (8)$$

where x = the number of fishes in the group.

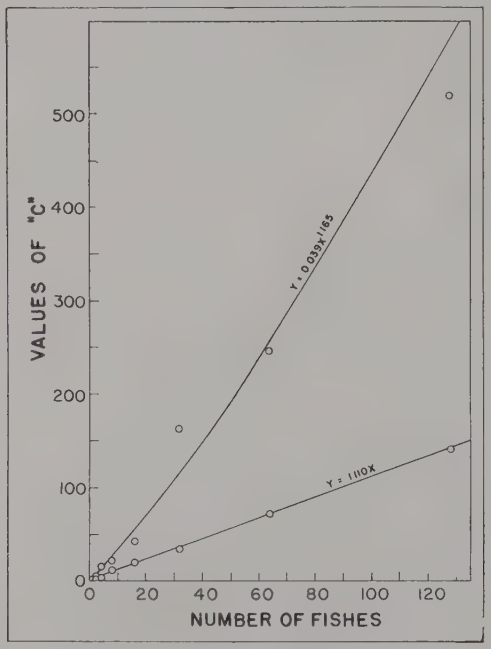

FIG. 6. Graph of data on *Oryzias* with reference to the equation $c = (f_1 p_1)(f_2 p_2)/t^2$. The circles represent actual values obtained through experiments which are tabulated in Table II. The two curves are graphic expressions of the equations $y = 0.309x^{1.165}$ and $y = 1.110x$. See text for full explanation.

This curve is shown in Figure 6 by the upper line passing through the deployment of points from Table II. Actually this is only a slightly better fit than a straight line would be. A similar equation derived for the other set of data yields the equation

$$y = 0.355\, x^{0.818} \qquad (9)$$

Here n is very close to unity and the fit is not nearly as good as when the equation for a straight line is employed, *i.e.* $y/x = \tan \Theta$ which becomes in the above notation, with $n = 1$, as follows:

$$y = 1.110\, x \qquad (10)$$

This is the lower line shown in Figure 6. It is extremely close to the observed values. It will be noticed in Table II that the calculated values depart fairly widely, especially in the higher values, as they must, in the case where the individual can see two groups. The increasing inaccuracy of the reactions of the observing fish in the presence of the larger numbers in both groups is evident. Where f_2 is = 2, 4, or 32, the observed values for c are greater than those calculated and all the rest are less. This could be interpreted to mean that the failure to reach calculated values when larger numbers of fishes were present was caused by the masking effect previously discussed. Under the conditions of the experiment it could not, in any case, have been very great for the test fish viewed the others through a glass partition about 9.5" long and not more than 6" high, while the width of the chamber containing the variable numbers of fishes was only 1.5". Since the fish used averaged 1" in length, the largest number used, 128, could have been spread out on such a sheet of glass without overlapping at any place. This is mentioned merely to give a clear picture of the situation, a condition under which the influence of very few if any fishes could have been eliminated by masking. In large schools the effect of this masking may be seen when a minor disturbance at one end causes a "shock wave" of sudden darting to surge through the school. This takes as appreciable time so that, under favorable circumstances, the fishes nearest the source of the disturbance will have returned to normal swimming while the "shock wave" is still traveling along at an apparently uniform rate in remote parts of the school. In schools below a certain size the information passes so rapidly to every individual that the behavior of the group appears to be explosive. The remarks of Rashevsky (1951a, 1951b) on imitative behavior and information transmission are clearly related to these considerations on the size of a school necessary to prevent each individual from being completely informed about the behavior of every other individual. Relating such matters to the study of the nature of fish schools and other animal groupings connects this work clearly with modern theories of communication through both animate and inanimate systems. See Shannon and Weaver (1949) for a pertinent exposition of the trends of current communication theories.

As indicated earlier the typical fish school is clearly made up of equipotential individuals. In such a group there is no appreciable "peck order" if any at all. Landau (1951) has developed a series of equations expressive of animal societies based on the nature of the "peck right." In his

notation the measure of hierarchy, h, is more than 0 where the individuals are not of equally aggressive potential. In the kind of social organization represented by the typical fish school, where the individuals have the same value in the above notation, $h = 0$. On purely mathematical considerations he indicates that the likelihood of a hierarchy being established decreases as the size of the group increases and beyond a certain size this likelihood becomes vanishingly small. Complementary to this would seem to be the condition that the lesser the tendency to build hierarchies, the greater would be the likelihood of large groups assembling. This is, of course, just what is shown by the typical passive attitude of schooling fish to their fellows as compared with the usual aggressive attitude of non-schooling fishes. Landau (1950) demonstrates mathematically that it is possible in a ". . . sufficiently large population, to have a stable behavior pattern which is quite independent of the desires of the population or of their inherent pattern of response." This is very suggestive in connection with the basic causes of school formation and on speculations concerned with their biological utility or its lack. This follows Rashevsky (1950, 1951c) who considers the effects of distance on imitative behavior where there is a choice of two mutually exclusive activities. In his notation the preferences, φ, may be either positive or negative, which condition leads to groups which show behavior in the central portion differing from that in the periphery. In the case of fish schools with φ not varying significantly from one individual to another the group should be substantially uniform throughout.

In the interesting work of Stewart (1947) on empirical mathematical rules concerning the distribution and equilibrium of populations the term d is used instead of d^2. The justification of this goes back to Lagrange who studied gravitational problems concerning more than two bodies, and comes down by way of Laplace and Poisson who were still concerned with celestial mechanics, through Green on magnetic poles and electric charge to Stewart (1941, 1947) on groups of human beings. An argument could be developed that in the present case the term d should not have been squared, and eventually it may be shown that such a change should be made. However, for the present preliminary purposes, at least, it was considered best to use the Newtonian or Coulombian value for the following reasons. In abstract the exponent of d could conceivably have any value, but for any aggregating objects it would not be expected to reach the third power for, as Newton himself pointed out, if it had obtained for the planets they would have moved off from the sun in spiral paths. In fact, another way in which the cohesiveness of a group of fishes might be shown would be to vary the value assigned to the exponent of d. Actually the curves shown in the figures, if d had not been squared, would still show the same general characteristics but the point of greatest curvature instead of being at or very close to the point of equilibrium would be displaced well into the negative range. That is to say reducing the size of the exponent of d lessens the sharpness of the change of direction near the zero value for c and increases the value of d where $c = 0$, somewhat similar to the increasing values of a as shown in Figure 4, but of course with differently shaped curves. Increasing the value of the exponent of d raises the point of maximum change in direction of the curve above the line of neutrality and sharpens the inflection again somewhat similar in appearance to Figure 4. Thus with d^2 the great strength of the repulsion appears on a very slight diminution of the distance beyond the equilibrium position, which would seem to be more truly indicated. With the present preliminary nature of these studies it would be pointless to attempt to delimit the value of this exponent into great refinement.

It is not the intent of this communication to apply these thoughts to an immediate problem, but this is published in its present form in the hope that it will stimulate others who may be more conveniently situated to carry forward this approach to the problems of animal aggregation in general.

Summary

1. An equation derived from consideration of schooling fish is presented as an instrument for comparative studies on social organisms.
2. The equation is:
$$c = a - (f_1 p_1)(f_2 p_2)/d^2$$
where d = distance between individuals or groups, f = number of individuals, p = potential of each individual, fp = repulsive force, a = attractive force and c = a measure of cohesiveness of the group.
3. A method of applying this to real schools is given, with an illustration of parameters of four different species.
4. A related equation
$$c = (f_1 p_1)(f_2 p_2)/t^2$$
where t represents amount of time in which the fishes show close approach and fp = attraction is referred to experimental data.
5. This indicates that the influence of a group

on one individual is directly proportional to the number in the group and may be expressed by the equation

$$c = k.x^n$$

where x = the number in the group and k and n are constants.

6. When there is a second group present the influence of the larger group on a single individual may be expressed by the same equation with different constants.

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SOIL PHOSPHATE AND THE DELIMITATION OF PLANT COMMUNITIES IN EASTERN AUSTRALIA

N. C. W. Beadle
Department of Botany, University of Sydney, Sydney, N.S.W., Australia

In a previous publication (Beadle 1953), mention was made of the role of soil phosphate in determining vegetation patterns in parts of Australia. In the account that follows the quantitative data which have led to this conclusion are presented.

Description of the Vegetation Pattern

In the Sydney district (climatic data, see Table I), the predominant vegetation type is a sclerophyllous forest dominated by species of *Eucalyptus;* two subformations are recognized (Prescott 1939), the wet sclerophyll and dry sclerophyll forests. Small areas are covered by subtropical rainforests. Within the dry sclerophyll forests or adjacent to them, large or small areas of xeromorphic scrub and heath commonly occur. The wet and dry sclerophyll forests are not only of different heights (Table II) and contain different species of *Eucalyptus* as dominants, but they differ also in the density and floristic composition of the subdominant strata. The wet sclerophyll forests include mesomorphic species, some of which are present also in the rainforest (including some lianas); the dry sclerophyll forests, on the other hand, contain a shrub layer of xeromorphs

TABLE I. *Climatic data for localities (or nearby stations) from which samples were collected. Temperature and humidity data for the last four stations are not available; they probably do not vary significantly from the figures quoted for Sydney. In all cases the rainfall is distributed fairly evenly throughout the year. Data supplied by the Commonwealth Meteorological Service, Sydney*

Station	Mean annual maximum temp. (°C)	Mean annual minimum temp. (°C)	Mean relative humidity (9 a.m.)	Mean annual rainfall (cms.)
Sydney Observatory	21.8	13.4	68	113.8
Riverview, Sydney	21.7	11.9	70	108.7
National Park	....	....	..	107.3
Sherbrook	....	....	..	145.1
Hornsby	....	....	..	106.6
Turramurra	....	....	..	127.6

with acicular, terete, or ericoid leaves, or with phyllodes or cladodes. The rainforest is made up of laurel-leaved plants, chiefly of Indo-Malayan origin, and is rich in epiphytes and lianas. The shrubs and heaths are composed of species characteristic of the shrub layer of the dry sclerophyll forests. All the xeromorphic species are typically Australian; most of them belong to the families Proteaceae, Myrtaceae, Leguminosae, Epacridaceae, and Rutaceae.

Similar conditions are reported elsewhere in Australia. Herbert (1951) in Queensland reports rainforest, sclerophyll forest, and mallee[1] within a few hundred yards of each other; Brough, McLuckie, and Petrie (1924), and McLuckie and Petrie (1927), describe rainforest on the basaltic soils of Mt. Wilson and dry sclerophyll forest on the sandstones nearby. The cause of all such patterns is possibly the same, but since the writer has data for the first-mentioned only, the discussion will be confined to the vegetation of the Sydney district.

Pidgeon (1940) working on the Hawkesbury sandstones of the Sydney district gives a very accurate description of the primary successions and the various climaxes. While the writer realizes the worth of Pidgeon's accounts, he cannot agree with her conclusions on the status of the various communities. Pidgeon arranges the communities as seres and describes as the climatic climax the *E. pilularis* (wet sclerophyll forest) association, which occurs in some of the valleys. The widespread dry sclerophyll forest (*E. gummifera—E. micrantha—E. sieberiana*) which occurs on the flats and ridges is described as a physiographic climax limited by soil depth. As far as the communities on shale are concerned (Pidgeon 1942), the same argument is followed: the soils derived from the shales, being deeper, support a taller and more mesomorphic vegetation.

With regard to soil depth, it is significant to mention here that, while very marked differences in soil depth from one rock type to another usually occur, the following points must also be taken into consideration: when soils are shallow, the trees almost invariably penetrate deeply into the parent material down crevices; secondly, when deep and shallow soils from the same parent material (such cases can be found, especially on the sandstones) and with the same topographic features lie close together, there is little or no change in the vegetation; thirdly, the deep soils of the valleys are not only deeper, but they have received additional nutrients washed down from above; fourthly, when only a small amount of clayey material derived from the shale is washed down over the sandstone, there is an increase both in size and degree of mesomorphism of the vegetation, even though the soil is still relatively shallow and boulders lie at the surface. These points throw doubt on the supposition that soil depth is all-important; they have led to an investigation of the nutrient levels of the various soils, and it is now concluded that the floristics and structures of the communities are determined either directly or indirectly by the phosphate content of the soil. An analogous condition is reported by Billings (1950) in North America, and a similar condition, but in a secondary succession, has been described by Allard (1942), who points out that available phosphate limits the rate of the secondary succession in woodland country in Virginia. The latter mentions also that the building up of soil nitrogen is governed by the phosphate level, which determines the invasion rate of nitrogen-fixing legumes. Parallel conditions are encountered in eastern Australia. It seems probable that the soil-phosphate level governs the activity of the *Rhizobia* in the legumes (which are abundant) and either directly or indirectly the degree of xeromorphism of the vegetation. It determines also the frequency of annual plants in the community, a point that was discussed in a previous publication (Beadle 1953). These conclusions are supported by three independent sets of experimental data, namely: (1) by the laboratory estimation of the relative fertility of the various soils; (2) by transplanting experiments; (3) by chemical analyses of leaves.

[1] A community dominated by dwarf species of *Eucalyptus*, usually 10-20 feet high.

TABLE II. *Showing the relationship between vegetation, soil, and soil parent material. The term "laterite" is used in the British, not in the American sense*

Geology	Predominant soil	Predominant vegetation	
		structure	dominant species
Narrabeen Group (Triassic) chocolate shale	brown forest	wet sclerophyll forests (80 to 120 feet high)	*Eucalyptus saligna, E. pilularis*
		rainforest	*Ceratopetalum apetalum, Doryphora sassafras*
Narrabeen Group sandstones and shales	gray and brown podsolic	wet sclerophyll forests (60 to 100 feet high)	*E. saligna, E. pilularis*
Hawkesbury sandstones (Triassic)	lithosols, iron podsols	dry sclerophyll forests (20 to 50 feet high)	*E. gummifera, E. sieberiana*
		wet sclerophyll forests in deep valleys only (60 to 80 feet high)	*E. pilularis*
		scrubs (6 to 20 feet high)	species of *Banksia, Acacia, Hakea, Leptospermum* etc.
Wianamatta Group (Triassic) shales	gray and brown podsolic	wet sclerophyll forest (60 to 100 feet high)	*E. pilularis, E. saligna*
Fossil laterite (Pliocene ?)	laterite	dry sclerophyll forests (20 to 50 feet high)	*E. gummifera*

(1). RELATIVE FERTILITY OF THE VARIOUS SOILS

Preliminary qualitative experiments on the soils, using tomato plants grown from seed in unfertilized soils, indicated that the nutrients in lowest supply are phosphate and fixed nitrogen. For the quantitative estimation of the relative levels of phosphate and fixed nitrogen a pot experiment (1 kg. of soil per pot) was designed using soils from different communities (see Table III), treated as follows:

a) control
b) nitrate only, added at the rate of 0.25 gm. NO_3 per 1000 gm. soil as KNO_3
c) phosphate only, added at the rate of 0.2 gm. PO_4 per 1000 gm. soil as KH_2PO_4
d) nitrate plus phosphate at the rate indicated in (b) and (c).

The pots were watered with distilled water and kept in the greenhouse at a temperature of 25-35°C for a period of six weeks. Flax was used as a test plant, being more tolerant than tomato of variations in pH and in soil texture. Each treatment was duplicated, and three plants were grown in each pot. After six weeks from sowing, the plants were harvested above the cotyledons, dried at 60°C and weighed (Table III). No adjustment has been made for the amount of dry matter produced by a flax plant in nutrient-free sand, except discarding the cotyledons. In nutrient-free sand, the plants averaged 18 mg. dry weight after six weeks' growth, which is higher than the mean weights of the plants grown in the least fertile soils, which are also the most acid. In view of this, the quantitative differences between fertility levels of the various soils are somewhat greater than the figures indicate; also, the level of readily available soil phosphate in the most infertile soils must approach zero.

The figures in Table III indicate clearly that, for the soils of the Sydney district, when a soil property is limiting, as is the case for all soils investigated except one, the limiting element is phosphorus. Soil nitrogen is not the primary limiting factor, as is commonly believed. In some cases, soil nitrogen is relatively high; this is probably the result of the high frequency of members of the Leguminosae. This effect of the legumes is particularly noticeable in the sample from the wet sclerophyll forest near Bola Creek, where *Acacia* spp. make up the entire shrub stratum. With increasing soil phosphate there is a decrease in the degree of xeromorphism of the community; thus rainforest composed of laurel-leaved plants occurs on the most fertile soils, and dry sclerophyll forests and scrubs composed of highly xeromorphic plants with leathery, terete, or acicular leaves, occur on the least fertile.

The data suggest that the segregation of the communities and the confining of individual species to distinct habitats are the result of differences in nutrient requirements. But this is not conclusive; other soil properties than those investigated experimentally and the factor "competition" cannot be overlooked at this stage. Transplant experiments, discussed in the next section, provide some information concerning these points.

TABLE III. *Mean dry weights (mgms) of flax plants (except Column 1) grown in soils from different communities under four different nutritional conditions. The figures in Column 1 are based on data for tomato plants. For the comparison to be made, the N + P treatment for the tomato plants has been taken as 150 and the other figures obtained proportionately. The data in this table are not accurate enough for quantitative estimates of nitrogen and phosphorus levels, but are to be used for comparative purposes only. For abbreviations, see Table II*

	Rainforest		Wet sclerophyll forest			Dry sclerophyll forest				Scrub
Locality	Bola Creek (National Park)	Sherbrook	Sherbrook	National Park	Turramurra	Loftus (National Park)	Hornsby	Terry Hills (Sydney)	Waterfall (National Park)	St. Ives (Sydney)
Soil parent material	Narr. choc. shale	Narr. choc. shale	Narr. shales	Narr. sandst. and shales	Wianam. shale	Hawk. sandst.	Hawk. sandst.	Laterite	Laterite	Hawk. sandst.
Control	160	80±19	43±11	37±1.4	33±4.5	28±4.2	23±5.2	25±1.2	13±0.4	16±2.2
NO_3 added	145	86	63±24	39±10	37±8.6	29±2.5	31±5.0	24±1.7	19±2.8	22±3.0
PO_4 added	160	115±23	65±13	132±38	91±20	45±4.1	82±1.4	37±3.7	93±9.3	19
NO_3 and PO_4 added	150	135±21	102±21	131±26	113±39	.....	.....	.....	130±9.1	

(2). Transplanting Experiments

Although only a limited number of transplant experiments have been done, the results are so consistent that the following generalizations may be made :—

When plants are transplanted (or grown from seeds) in soils of higher fertility than those in which they occur naturally, growth is vigorous and flowering and fruiting satisfactory, provided no competitors native to the new soil are present. The reverse, however, is not true. For example, species of *Eucalyptus, Banksia, Callistemon, Melaleuca, Grevillea, Hakea,* etc. native to the skeletal soils of Hawkesbury standstones can be grown successfully on the podsols of the Wianamatta shale. On the other hand, species from the rainforest, *e.g., Brachychiton acerifolium, Alphitonia excelsa* do not survive when transplanted to sandstone soils, while on soils derived from the Wianamatta shale they merely survive, growing at such a slow rate that it is doubtful if they could compete with the natural vegetation of the area. When plants are transferred to soils of higher fertility, the growth rate is markedly increased, leaf size is increased and leaf thickness is decreased. Similar increases in growth rate, and leaf size have been produced by the addition of nitrate and phosphate to plants growing in their own soil (Williams 1952). Similarly, plants typical of soils of high fertility can be grown on soils of low fertility if additional fertilizer is added.

These transplant experiments, together with the fertilizer trials, lay stress on the importance of nutrients in the distribution of the various species found in the several communities native to the Sydney district. They suggest furthermore that each species has a minimum nutrient requirement which must be satisfied if the plant is to grow, reproduce and compete with other species in the area. Additional evidence to support this view is given by the chemical analyses of the plants, as discussed in the next section.

(3). Chemical Analyses

Chemical analyses have dealt mainly with the percentage ash and the percentage phosphate in the leaves. The results of these analyses are summarised in Table IV. The figures indicate that the component species within any community are similar with respect to the percentage ash in the leaves, and, more particularly, to the percentage phosphate. Furthermore, the highest concentrations of both constituents are found in the most mesomorphic communities and the lowest concentrations in the most xeromorphic. When a plant species occurs in more than one distinct community, both ash and phosphate contents of the leaves vary. The highest figure occurs in the most mesomorphic community.

As far as the total ash is concerned, it is relevant to mention here that these figures are not necessarily indicative of the mineral requirements of the plant, since sodium invariably makes up a significant percentage of the ash. Furthermore, several of the species dealt with in this paper accumulate aluminum, a point which has been given considerable attention by Webb (1953). Complete analyses for the individual bases in the ash samples have not yet been done; however, from data available (unpublished) it is doubtful whether this information will be of any great significance.

More detailed results of chemical analyses, which are being extended to the organic constituents, are to be published shortly by the writer and co-workers in a series of papers dealing with xeromorphs.

TABLE IV. *Percentage ash (A) and phosphate as PO_4 (P) in oven-dry leaves of various species from different communities. Leaf samples for these analyses were collected from the same areas as the soils in Table III*

Species	Rain forest				Wet sclerophyll forest						Dry sclerophyll forest			
	Bola Creek (National Park)		Sherbrook		Sherbrook		National Park		Turramurra		On Hawkesbury sandstone		On laterite	
	A	P	A	P	A	P	A	P	A	P	A	P	A	P
Panax murrayi F. Muell.	12.4	0.64												
Diploglottis cunninghamii J. Hook.	8.6	0.67												
Claoxylon australe Baill.	14.2	0.86	16.1	0.54										
Doryphora sassafras Endl.	8.5	0.45	5.6	0.19										
Eugenia smithii Poir.	5.7	0.32	4.4	0.26										
Ceratopetalum apetalum Don.	7.2	0.28	6.5	0.18										
Acacia binervata DC.			3.5	0.25	3.7	0.17								
Eucalyptus saligna Sm.					5.6	0.32	4.6	0.47	4.7	0.35				
E. pilularis Sm.					2.9	0.23			4.3	0.17				
Syncarpia laurifolia Ten.					2.9	0.09			3.0	0.11				
Acacia impleza Benth.									4.4	0.20				
Eucalyptus gummifera (Gaertn.) Hochr.											2.8	0.09	3.2	0.13
E. sieberiana F. Muell.											2.3	0.12		
Banksia serrata Linn.											2.2	0.10	2.2	0.07
Daviesia latifolia R. Br.											2.9	0.06	1.9	0.05
Hakea dactyloides Cav.											1.9	0.06	1.9	0.05
Persoonia salicina Pers.											2.4	0.07	2.2	0.07

DISCUSSION

The above data indicate that for the communities of the Sydney district, soil fertility is primarily responsible for the delimitation of the various plant communities; soil phosphate is the factor which selects the vegetation, with the possible exception of certain of the small patches of rainforest which may be climatically controlled. It appears that each species has a minimum requirement for normal growth, and if this requirement is fulfilled the plant survives in the area, provided it can compete with other species. Plants with low mineral requirements appear to be excluded from the more fertile soils because of their inability to compete with the more vigorous species native to these soils; a segregation of species naturally results.

The figures in Table III indicate that soil nitrogen, though often low, is never a limiting factor. Indeed Hannon (1949 and unpublished data) has shown that total soil nitrogen may reach relatively high levels in communities of extreme xeromorphs. This is consistent with the fact that a very high percentage of the plants of the dry sclerophyll forests and of the scrubs and heaths are members of the Leguminosae; these plants nodulate in the field and grow well under laboratory conditions in nitrogen-free sand culture, if *Rhizobia* are introduced into the sand (Hannon 1949).

That species are selected by the soil because of differences in mineral requirements of the plants is well illustrated by the rainforests and floristically related communities. The richest of the rainforest dealt with here (Bola Creek) contains some 40 mesomorphic species; it occurs on the most fertile soil (derived from the chocolate shales). With decreasing soil fertility, not only does the number of species decrease, but the community becomes lower and the canopy becomes more open. These depauperate rainforests grade into wet sclerophyll forest in which sclerophyllous eucalypts constitute the upper stratum, and mesomorphic plants (sometimes components of the rainforest also) make up the shrub layer. This leads to the interesting problem of rainforest migration: the spread of rainforest has been recorded from very many situations in Eastern Australia (*e.g.*, Fraser and Vickery 1939). Such migrations are detected by the occurrence in *Eucalyptus* forest of young plants typical of the rainforest and by the presence in well grown rainforest of very old (but no young) trees of *Eucalyptus*. These migrations are usually accounted for by changes in climate—an increase in either rainfall or humidity of the macroclimate or of the microclimate in the ecotone between rainforest and sclerophyll forest. In some cases this may be the explanation. On the other hand, the migration could well result from a change in nutrient levels in the area adjoining the rainforest. The mechanism is probably as follows: since rainforest species contain a higher percentage of nutrients in their leaves than do the plants of the adjoining forest, any leaf material carried from the rainforest to the sclerophyll forest must eventually enrich the soil; in time the soil of the sclerophyll forest becomes sufficiently high in nutrients to support those rainforest species with the lowest requirements; these species migrate, and the process continues. A similar migration of rainforest occurs as the result of concentration of nu-

trients in valleys. This is well illustrated on the Hawkesbury sandstones where valleys sometimes support patches of depauperate rainforest dominated by species with a relatively low nutrient requirement (notably *Ceratopetalum apetalum*); in contrast, equally wet areas on soils of comparable depth on the hilltops (e.g., around or below hanging swamps), where no such concentration of nutrients can occur, support dry sclerophyll forest.

Summary

The role of soil phosphate in delimiting communities is discussed; the higher the phosphate content of the soil, the more mesic and taller is the vegetation. This conclusion is supported by quantitative data on the relative fertility of the soils, by transplant experiments and by chemical analyses of the ash of leaves.

Acknowledgments

The writer is indebted to Professor J. McLuckie and to Dr. H. S. McKee for their criticism of the manuscript.

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THE ECOLOGICAL DISTRIBUTION OF THE *PEROMYSCUS LEUCOPUS* SPECIES GROUP IN EASTERN TEXAS[1]

W. H. McCarley

Department of Biology, Stephen F. Austin State College, Nacogdoches, Texas

Two species, *Peromyscus leucopus* and *P. gossypinus*, make up the species group *leucopus* of the genus *Peromyscus* (Osgood 1909). The species *leucopus* includes mice that are commonly called wood-mice and the species *gossypinus* includes mice that are commonly called cotton-mice. Wood-mice are widely distributed over North America, occurring as far north as Nova Scotia, as far west as Montana and Arizona, and extending southward into southern Mexico. Cotton-mice, however, are restricted in their geographic distribution to the Gulf Coastal Plain from eastern Texas to the Atlantic Ocean. In parts of Virginia, North Carolina, South Carolina, Georgia, Alabama, Mississippi, Tennessee, Arkansas, Kentucky, Louisiana, Oklahoma, and Texas the geographic ranges of *leucopus* and *gossypinus* overlap broadly. Because these two species are closely related and, in part, occupy the same geographic range, they are here considered sympatric species.

Comparatively few studies have been made on the biological relationships of these two species. Howell (1921) found four individuals in Alabama that he considered to be natural hybrids between *leucopus* and *gossypinus*. Dice (1937) studied the fertility relations of the two species in the laboratory and found that they were interfertile and produced fertile hybrids. Later, Dice (1940) published the results of a morphological and, to some extent, ecological study of *leucopus* and *gossypinus* in the Dismal Swamp region of Virginia. Calhoun (1941) studied the food habits

[1] Presented as a portion of a doctoral dissertation at the University of Texas.

of the wood-mouse and the cotton-mouse in the vicinity of Reelfoot Lake in Tennessee.

Because these two species occur together in many localities it was believed that a comprehensive study of the relations of *leucopus* and *gossypinus* would reveal the mechanisms whereby two species so closely related as to be interfertile are able to occur together and still maintain their species-distinctness. The accessibility of the two species in eastern Texas offered an excellent opportunity to study the biological relationships of these two species in nature. This paper is a report of the ecological preferences and distribution of the two species in eastern Texas and is based on field studies extending from September, 1950 until August, 1952.

The author wishes to express his thanks to Dr. W. F. Blair for his invaluable advice during the course of this problem.

Region Studied

The region in which the ecological distribution of *Peromyscus leucopus* and *P. gossypinus* was studied in the field involves an area of approximately 28,000 square miles in eastern Texas; it is generally known as the East Texas timbered region. This area extends from the Red River in the north to the coastal prairie in the south. On the east the region in which field work was done was arbitrarily limited at the Texas-Louisiana border. On the west the region studied is delimited by the characteristic blackland prairie of central Texas. The majority of the East Texas timbered region is classified by Thornthwaite (1948) as a B_1 (humid) climate. In the B_1 climate there is a moisture-surplus index of 20 to 40 per cent.

The East Texas timbered region is generally considered to have three distinct vegetational types (Tharp 1926). These are as follows: (1) the pine forest in the southeastern portion, (2) the pine-oak forest in the central and northern part and which is the most extensive, and (3) the oak-hickory forest which constitutes the western part of the East Texas timbered region.

The pine forest is characterized by the occurrence of long-leaf pine (*Pinus palustris*), loblolly pine (*P. taeda*), and short-leaf pine (*P. echinata*), listed in the order of their decreasing abundance. These three species are considered by Tharp to be the climax vegetation in the pine forest of eastern Texas.

The pine-oak forest is considered by Tharp to be an ecotone between the pine forest and the oak-hickory forest. The pine-oak forest is characterized by the occurrence of loblolly pine, short-leaf pine, postoak (*Quercus stellata*), and hickory (*Carya* sp.).

The oak-hickory forest of eastern Texas extends as a narrow strip between the pine-oak forest and the blackland prairie of central Texas. It is nowhere more than 60 miles wide and it extends from Waller County in the south to the Red River in the north (Tharp, *op. cit.*). The one species that is dominant throughout the better drained areas is the postoak. Blackjack (*Quercus marilandica*) and hickory (*Carya* sp.) are usually scattered through the stands of postoak.

In the East Texas timbered region, mice of the *Peromyscus leucopus* species group are ordinarily restricted to timbered areas. The forested areas of this region can generally be divided into two distinct habitats. These two habitats are designated as the upland forest habitat and the lowland forest habitat according to the natural distribution of the dominant woody species. These two habitats are present in varying admixture throughout the East Texas timbered region.

The lowland forest habitat is the most mesic habitat in eastern Texas. It occurs wherever there is sufficient moisture to support the dense growth of woody and herbaceous vegetation that is characteristic of the lowlands of the Gulf Coastal Plain. The lowland forest habitat is limited to the floodplains of the numerous streams which drain the East Texas timbered region. The dominant vegetation of the lowland forest generally consists of the following trees, listed in the order of their decreasing abundance: water oak (*Quercus nigra*), willow oak (*Q. phellos*), sweet gum (*Liquidambar styraciflua*), black gum (*Nyssa sylvatica*) and birch (*Betula nigra*). In some areas, particularly in the pine forest region, cypress (*Taxodium distichum*) and magnolia (*Magnolia grandiflora* and *M. glauca*) are among the dominants. In the western part of the oak-hickory forest the lowland vegetation consists of species of elm (*Ulmus* spp.), pecan (*Carya pecan*), cottonwood (*Populus deltoides*) and sycamore (*Platanus occidentalis*). Large numbers of fallen and uprooted trees in various stages of decay are usually present in the lowland forest habitat. There are numerous swamps, sloughs, and oxbow lakes in these lowlands and the water table is usually only a few feet below the surface. All of these factors contribute to the maintenance of the mesic growth of hardwoods. The lowland forest habitat is most extensive in the pine forest region and least extensive in the oak-hickory forest region.

The upland forest is the most xeric natural vegetational type in eastern Texas. It generally occurs on the slopes and summits of the hills.

Here, there is always an insufficient amount of available moisture to support typical plant species of the floodplains. The soil of the uplands is generally low in mineral plant nutrients and organic matter. These factors plus the more xeric conditions do not allow as dense a growth of vegetation as in the lowlands. The number of species and individuals comprising the mammalian fauna of the upland forest is also generally smaller than in the lowland forest. The dominant vegetation of the upland forest habitat varies with the three vegetational regions. In the pine forest the dominant vegetation is the same as the climax vegetation and the subdominant vegetation is usually made up of postoak, blackjack, and wax myrtle (*Myrica cerifera*). In the pine-oak forest the dominant vegetation is usually short-leaf pine, loblolly pine, and postoak. Blackjack, hickory, and sassafras (*Sassafras sassafras*) make up the subdominant vegetation in the pine-oak forest. In the oak-hickory forest the dominant vegetation of the uplands is, almost without exception, postoak, followed in some places very closely by blackjack and hickory. The upland forest habitat is most extensive in the oak-hickory region and least extensive in the pine forest region.

Methods

Twenty-six localities in eastern Texas, distributed in 15 counties (Table I) were studied in an attempt to determine the ecological preferences and distribution of the two species in this region. These localities were selected for several reasons; geographic position, presence of the upland and lowland forest habitats in the same locality and general accessibility. In studying these localities it was the practice to make a sketch map of the immediate area to show the approximate distribution of the upland and lowland habitats. Live traps and/or snap traps were set in lines that extended from the uplands into the lowlands. In so far as was possible the traps were distributed equally in each of the two habitats. The location of these trap lines was also plotted on the sketch maps, as was the site of capture of each individual. This made it possible to establish for each locality the ecological preference of each individual that was caught and also to ascertain to a certain extent the relative abundance of each species.

Ecological Relations and Distribution

The wood-mouse is apparently one of the rarest small mammals in eastern Texas. This is indicated by the fact that only 23 individuals were collected in 4117 trap nights in 26 localities where they would be expected to occur. The species probably occurs throughout eastern Texas, but at least in the period from 1950 to 1952, it was never very abundant. It is probably significant that Bailey (1905) did not record any specimens of *leucopus* from the East Texas timbered region. From east to west in the oak-hickory forest region, *leucopus* gradually becomes more abundant until, in the western part of this region and beyond the western limits of the geographic range of *gossypinus*, it becomes the dominant *Peromyscus* in the woodlands.

The cotton-mouse is by far the more abundant of the two species and is probably the most abundant small mammal over its geographic range in eastern Texas. It apparently reaches its western geographic limits in the oak-hickory forest approximately on a line drawn through the western parts of Henderson and Brazos counties. Specimens of *gossypinus* were collected in all of the counties studied with the exception of Brazos and Jasper.

In the area studied the wood-mouse is apparently restricted to the upland forest (Table I). In the western part of the oak-hickory forest this species is known to occupy the lowland forest habitat but no specimens of the cotton-mouse have been collected as far west as the localities where the wood-mouse has been found to occur on the floodplains. Where the geographic ranges of *leucopus* and *gossypinus* overlap in Texas, *leucopus* has been taken only in the upland forest habitat.

Table I. *Distribution of* Peromyscus leucopus *and* P. gossypinus *in upland forest and lowland forest habitats in eastern Texas as determined by trapping records*

County	No. of Trap Nights Up.	Low.	No. of *leucopus* caught in Up.	Low.	No. of *gossypinus* caught in Up.	Low.	No. of Localities
Anderson	300	300	2	0	1	8	1
Brazos	0	172	0	1	0	0	1
Cherokee	500	630	0	0	0	20	6
Harrison	606	695	6	0	11	6	1
Henderson	277	285	8	0	1	40	3
Houston	200	200	0	0	0	3	1
Jasper	125	400	0	0	0	0	1
Nacogdoches	669	1141	1	0	11	104	5
Newton	900	900	5	0	0	4	1
Polk	100	100	0	0	0	2	1
Rusk	200	210	0	0	0	1	1
Sabine	50	100	0	0	0	2	1
Shelby	100	100	0	0	0	2	1
Titus	40	40	0	0	0	1	1
Walker	50	74	0	0	0	1	1
Total	4117	5347	22	1	24	194	26

The ecological distribution of *gossypinus* is not so easily defined as that of *leucopus*. Trapping records (Table I) indicate that *gossypinus* occurs

predominantly in the lowland forest and only occasionally in the uplands. With the exception of the record in Harrison County, all of the *gossypinus* individuals collected in the upland forest habitat were found there during the months of January, February, and March. At no place was *gossypinus* found in the uplands unless there was a population of *gossypinus* in the immediately adjacent lowlands. It is significant that the months of January, February, and March are ordinarily the months in which the *gossypinus* populations of eastern Texas reach their peak of highest population density (McCarley *in press*). Howard (1949) demonstrated that *Peromyscus maniculatus* populations in southern Michigan exhibited a negative response to crowding and that the rate of dispersal increased as the population density increased. Such a response might, in part, explain this seasonal occurrence of *gossypinus* in the upland habitat.

Caddo Lake State Park in Harrison County was studied at three separate times, and the *Peromyscus* populations here exhibited a different ecological distribution from those of similar populations elsewhere. In June of 1951, cotton-mice were found in both the upland and the lowland forest habitats while wood-mice were found only in the upland forest habitat. In February of 1952, the area was again studied and *gossypinus* was found to be present only in the upland forest. No *leucopus* was taken at this time. In June of 1952, the area was again studied, and while no *leucopus* was taken, *gossypinus* was collected in both the upland and the lowland forest habitats but predominantly in the uplands.

In order to obtain more specific information on the ecologic preferences of the two species, ten adult *leucopus* (five males and five females) and ten adult *gossypinus* (in the same sex ratio) were marked and released in a partially isolated tract of timber, 15 miles northwest of Nacogdoches, Texas. This tract of timber covered approximately eight acres and was partially isolated from other areas of timber by open cultivated fields. At the time of the study these fields were covered by a sparse growth of crimson clover and hairy vetch. The only natural dispersal routes connecting the study plot with other timbered areas were two fence rows which were partly grown up in postoak. The nearest timbered area to the study plot was about 250 yards away. The study plot was divisible into the upland and lowland forest habitats (Fig. 1) and the dominant vegetation of these habitats was typical of the vegetation previously described for these habitats in the pine-oak forest. Between March 12 and 17, 1952, the study plot was trapped thoroughly to remove any individuals of *leucopus* or *gossypinus* that might be living there. Live traps were set on the afternoon of March 17, in a grid pattern, 75 feet apart. As soon as it was dark the 20 marked mice were released in the center of the quadrat. It was believed that 20 individuals would probably overpopulate the area with the result that some of the mice would disperse. Live trapping continued from March 17 until March 27, 1952. Mice recovered two or more times were considered to have established residence on the study plot. Those mice which were not recovered or which were recaught only once were considered to have dispersed.

On the first day after the release of the mice,

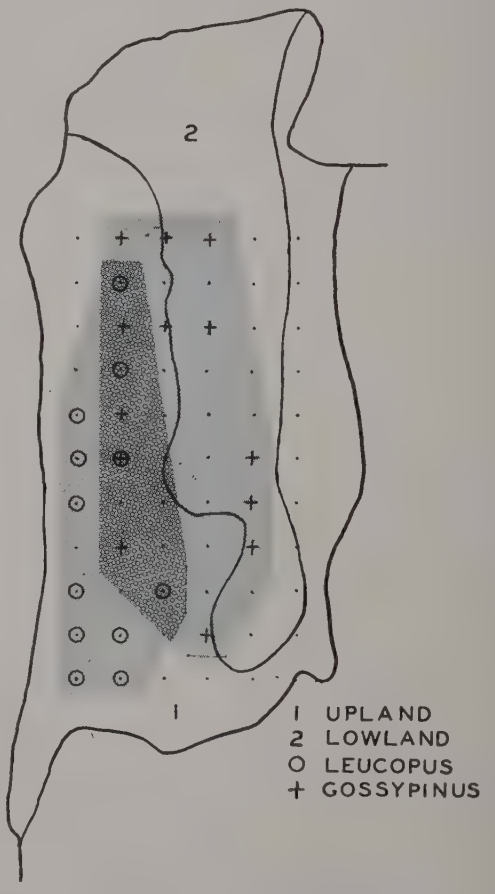

FIG. 1. Outline drawing of a partially isolated tract of timber, 15 miles northwest of Nacogdoches, Texas, showing the distribution of the upland and the lowland forest habitats and the sites of capture and distribution of released *Peromyscus leucopus* and *P. gossypinus* at the end of ten days of trapping.

two *leucopus* and five *gossypinus* were recovered. On the fifth day of trapping, three *leucopus* and five *gossypinus* had established residence on the study plot and at the end of the tenth day of trapping, five *leucopus* and five *gossypinus* had established residence on the study plot. At this time the study was discontinued because of the death in the traps of the majority of the resident animals. On March 28 the traps were removed from the study plot and were set in likely places in the surrounding area in an attempt to recover those individuals which had dispersed. No marked individuals were recovered in ten nights of trapping.

This experiment suggests that the two species have fairly distinct preferences for certain types of habitats. In general, the *leucopus* established themselves in the upland habitat. An outline drawn around their combined home ranges in accordance with the method proposed by Blair (1940) shows that their distribution barely made contact with the lowland habitat (Fig. 1). On the other hand, the *gossypinus* did not arrange themselves in quite so definite a relationship with the lowland habitat as did the *leucopus* with the upland habitat. Approximately one-half of the combined home ranges of the *gossypinus* individuals, calculated in the same manner as those of the *leucopus* individuals, lies in the upland habitat and overlaps to a considerable extent the ranges of *leucopus* (Fig. 1). These results constitute additional evidence that in eastern Texas, *leucopus* is restricted to the upland forest habitat whenever it occurs in the same area with the cotton-mouse. On the other hand, it seems that *gossypinus* prefers the lowland forest habitat but may establish itself in the upland habitat if overcrowding forces a dispersal from the preferred lowland habitat.

The ecological distribution exhibited by *leucopus* and *gossypinus* in eastern Texas is generally similar to that which has been reported for these two species in other parts of the southeastern United States. Howell (1921) found that in Alabama *leucopus* was partial to the higher drier uplands while *gossypinus* occupied a variety of habitats but was more numerous in the swamplands. In the Reelfoot Lake region of Tennessee, Calhoun (1941) found that *leucopus* was limited in its distribution to areas that were not subject to inundation by floodwaters, whereas the majority of *gossypinus* were trapped in areas that were subject to annual flooding. The borders of these habitats overlapped sufficiently so that both species were occasionally taken in the same trap. Dice (1940) found a somewhat different situation in the Dismal Swamp region of Virginia. Here, *gossypinus* appeared to be entirely limited to the swampy and marginal types of habitats but *leucopus* occurred in both the uplands and the lowlands.

Summary

The ecological distribution of *Peromyscus leucopus* and *P. gossypinus* was studied in eastern Texas. Results of field studies from 1950 until 1952 indicate that in eastern Texas, *leucopus* is restricted to the upland forest habitat wherever it occurs in the same area with *gossypinus*. *Peromyscus gossypinus* occurs predominantly in the lowland forest habitat, but, during peaks of high population density, dispersal forces some *gossypinus* individuals into the upland forest habitat.

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SOIL MANTLE MOVEMENT IN RELATION TO FOREST CLEARING IN SOUTHEASTERN QUEENSLAND[1]

LINCOLN ELLISON AND J. E. COALDRAKE
Intermountain Forest and Range Experiment Station, U. S. Forest Service, Ogden, Utah, and Division of Plant Industry, Commonwealth Scientific and Industrial Research Organization, Brisbane, Queensland

Landslides have been conspicuous on certain cleared slopes of southeastern Queensland for many years and particularly since heavy rains in 1950 and 1951 (Fig. 1). The slides are generally—indeed, almost universally—attributed to loss of binding tree roots following removal of forest. The belief prevails, not only among farmers and technicians in southeastern Queensland, but in literature pertaining to landslides elsewhere, that mass movement is restrained under forest much more effectively than under grass.

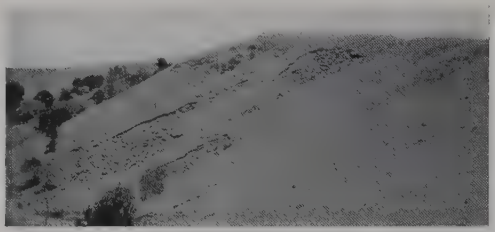

FIG. 1.—Landslides between Nambour and Mapleton. These slopes, which once supported rainforest, have been cleared and sown to paspalum pasture. December 11, 1951.

We have been able to find little factual evidence in the literature bearing on the effects of clearing, however, either in the form of measurement or qualitative description. Do landslides ever occur on steep slopes under rainforest? What sort of soil movement does occur there? Could it be that landslides are as common under rainforest as on cleared ground, but are not seen because of the screen of treetops and the difficulty of getting through the forest on foot? These and related questions led to the inquiry reported here.

Within the area of study indicated in Figure 2, we have been concerned with slopes which, for the most part, supported rainforest prior to clearing. Most landslides are found on such slopes. Our method of study has been observational, simply a comparison of the evidence of soil movement under rainforest with that in cleared pasture. Rainforest in more or less undisturbed condition has been observed on three sites on the Maleny Plateau, on Mt. Mee, Mt. Glorious, Mt. Tamborine, part of the Lamington National Park near Binna Burra, Numinbah Falls National Park, and two sites near the head of Richmond River in New South Wales. Landslides have been observed on cleared ground in the same localities.

VEGETATION

"Rainforest," as the term will be used here, refers to Australian subtropical rainforest. It has a characteristically dense, elevated canopy and a scant understory (Fig. 3). The trees are of many genera: *Ackama, Araucaria, Archontophoenix, Argyrodendron, Baloghia, Brachychiton, Castanospermum, Cedrela, Citronella, Cryptocarya, Dissiliaria, Eugenia, Ficus, Flindersia, Grevillea, Laportea, Litsea, Podocarpus, Sloanea,* and *Synoum* are perhaps the commonest. Lianas and fern-epiphytes are abundant. Figure 3 gives an idea of rainforest structure, but unfortunately it is not possible to capture in a photograph the subdued light, high humidity, and equable temperature that characterize the distinctive environment beneath a rainforest canopy. Local names for rainforest (a term, incidentally, almost never used by countrymen) include "scrub," "softwood scrub," and "vine scrub," all of which are singularly inappropriate to such lofty forest growth.

Eucalypts are conspicuously absent from this rainforest, except in the ecotone and where inliers of eucalypt forest are still being engulfed by rainforest. Here large trees of *Eucalyptus grandis* or *Tristania conferta* may occur; from the size of these trees and their lack of reproduction it is evident that rainforest is encroaching on eucalypt forest on such sites. Other common species of *Eucalyptus* near rainforest are *E. pilularis, E. microcorys, E. paniculata,* and *E. resinifera.*

The commonest sown pasture grass on cleared ground is *Paspalum dilatatum.* Kikuyu grass

[1] This exploratory study was made during the latter half of the senior author's visit to Australia from August 1951 to May 1952 as a Fulbright Research Fellow sponsored by the U. S. Educational Foundation in Australia and the Division of Plant Industry, C.S.I.R.O. The authors would like to acknowledge individually the help generously given by many people, but the list of names is too long. It includes farmers, members of the Department of Geology, University of Queensland, of the Commonwealth Meteorological Bureau, of the Queensland Main Roads Commission, and of the State forest services of Queensland and New South Wales.

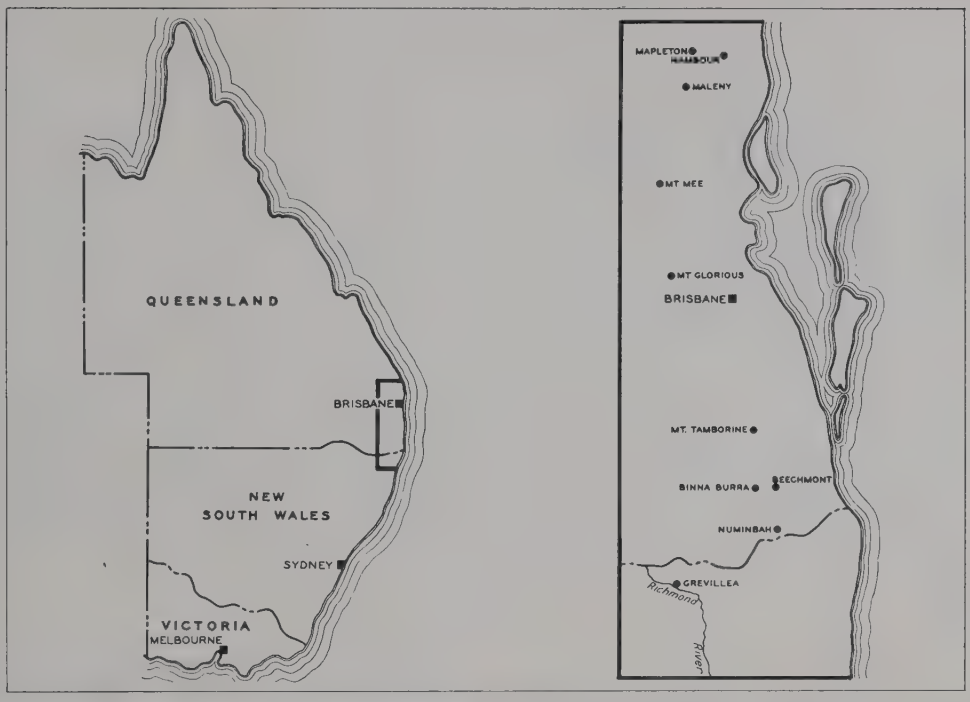

FIG. 2.—Southeastern Queensland showing localities mentioned in text.

FIG. 3.—Rainforest, Mt. Glorious. The lattice effect is provided by roots of strangling figs. Lianas and epiphytes, particularly massive ferns, are abundant. April 10, 1952.

(*Pennisetum clandestinum*) and Rhodes grass (*Chloris gayana*) are also common in some localities. These grasses form a heavy turf, to the exclusion of most other species (Fig. 1).

The introduced shrub, *Lantana camara*, invades cleared ground such as abandoned banana plantations, roadsides, and poorly maintained pasture. It commonly forms dense thickets at the margins of rainforest and cleared ground, or in rainforest openings, and may extend as an almost impenetrable undergrowth into *Eucalyptus-Tristania* forest.

ENVIRONMENT

The Maleny Plateau will be used as an example of landslide country. It rises sharply above the adjoining coastal plain to elevations of 1,300 to 1,700 feet above sea level. Slides are particularly numerous on its flanks, and a few fairly undisturbed areas of rainforest may still be found on these slopes. The plateau was first logged of its best timber, which opened parts of the canopy temporarily. Then, beginning about 1900, forest on the most desirable land was felled and burned to make way for crops and pastures. Clearing went forward particularly rapidly about the time of World War I, and to some extent it continues today. Many tracts were planted to bananas first and later sown to pasture, and some steep slopes

where cultivation has been discontinued have become clothed with dense thickets of lantana. In other areas weeds, principally lantana, have invaded pasture, rendering it useless.

Rainfall at Maleny, which is normally concentrated in summer, amounts to about 74 inches annually. In February and July 1950, and in January 1951, rainfall was greatly in excess of average (Table I).

TABLE I. *Monthly rainfall totals at Maleny, Queensland, for 1950 and 1951, in comparison with the 35-year average, 1915-1949; units are inches*

	1950	1951	35-year average
January	13.35	35.45	10.43
February	32.52	10.86	11.09
March	15.68	16.82	10.84
April	7.70	1.19	8.20
May	3.26	1.65	5.18
June	7.40	2.27	3.99
July	25.81	0.24	2.72
August	4.02	0.82	1.82
September	1.14	0.66	2.82
October	6.14	4.93	3.90
November	8.78	0.95	4.81
December	11.51	2.95	8.15
Total	127.31	78.79	73.95

Although residents of the Maleny district agree in associating landslides with these wet years, we have been unable to discover precise dates for the slides. Probably most slides occurred with heavy daily falls following prolonged periods of rain. Thus on February 28, 1950, 9.05 inches fell immediately following two days of more than 3 inches each, or 20 consecutive days of rain amounting to 23.38 inches. Again, on January 31, 1951, 12.30 inches fell after six days totalling 19.60 inches with falls of 4.75 and 7.60 inches the two days immediately preceding. According to the *Nambour Chronicle*, one of the main roads was blocked by slides on the day of heaviest rainfall. Another heavy fall occurred later in the same summer: between March 12 and 20, 15.91 inches fell, and of this amount 8.95 inches fell March 19.

Heavy rainfall in winter is less common, but 6.25 inches fell June 20-23, 1950, 5.26 of this on the last day. Again there were only three days without rain in the 22-day period July 9-August 1, 1950, when 26.74 inches fell, including 4.67 inches July 20 and 4.34 inches July 28.

The Maleny Plateau is formed of Tertiary basalt overlying Mesozoic sedimentary rocks, at least in the eastern portion.[2] The top of the plateau is rolling, with gentle slopes for the most part, and has practically no landslides. The sides of the plateau are steep, except where they are interrupted by terraces (Fig. 4), and are marked by large numbers of landslides. From the numerous slump scarps and down-thrown surfaces that can be seen, mostly of great age, it is clear that progressive collapse of the edges of the basaltic cap and of the rocks underlying the terraces has been an important part of the landforming process (Fig. 5). Most of the landslides of 1950 and 1951 occurred on these slopes, but the collapse of overlying caprock was not involved.

The soil of the top of the plateau is red, a deep, permeable clay loam, practically free of rock. The soils on the flanks of the plateau are comparatively shallow, a dark brown solum perhaps eighteen inches deep overlying a yellowish brown or grayish subsoil that is evidently weathered to considerable depth. These slope soils are very rocky, often containing a considerable volume of basaltic boulders that have been rounded by weathering. That they are much less permeable than the red soils of the plateau top is indicated by the stickiness of the clay subsoil, oozing of water in springs and seeps, and ponding of water in hollows.

The low permeability of this subsoil is evidently an important factor in promoting mass movement, causing water to flow laterally within the upper portions of the mantle[3] and lubricate a slip surface. This, as is indicated by the sliding and flowing that occurs on the terraces with their low gradients, is evidently the chief reason for the greater incidence of landslides on the shallower, dark brown soil of the sides of the plateau than on the red soil at the top. Steepness of slope is important, too, for many landslides occur on steep slopes; but the occurrence of slides and flows on moderate slopes suggests that the disposition of water within the mantle is the controlling factor. Recent slumps are particularly common in the steep heads of small drainages: here, doubtless, the maxima of slope steepness and of subsurface accumulation of water are combined.

OBSERVATIONS

The point has been made that slumping is an important geomorphic factor at the edges of these plateaus. The evidence of large slumps can be seen readily on cleared ground. Infinite gradations from fresh roughness to aged gentleness in their relief indicate that slumps have been occurring over a long time, and one may well conclude that most of them antedate clearing of the forest. If this evidence were not enough, many old

[2] Personal communication, Prof. W. H. Bryan, Department of Geology, University of Queensland.

[3] The term "mantle" is used to include both soil and fragmental parent material or rock waste lying above bedrock.

FIG. 4.—A portion of the eastern scarp of the Maleny Plateau showing an extensive terrace formed by erosion-resistant sedimentary rocks underlying the basaltic cap. Recent slumps and flows have been even more extensive on the moderate terrace slopes than on the steep slopes above. Considerable water oozes to the surface on the the terrace in seeps and ponds. April 16, 1952.

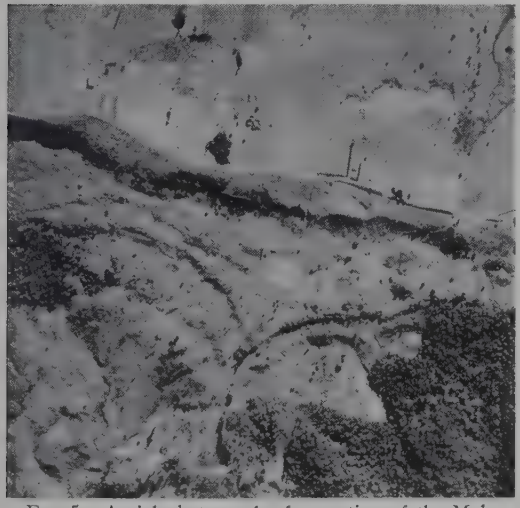

FIG. 5.—Aerial photograph of a portion of the Maleny Plateau, showing how the topography has been conditioned by slumping of the basaltic cap to produce several terraces. The extent of change in vegetal cover may be gauged from the contrast between uncleared rainforest (lower right and left center) and pasture in center. Photograph by Adastra Airways.

slumps can be found on slopes in rainforest. Some of these old slumps are very large, presumably resulting from collapse of resistant, overlying beds following sapping of the slopes below. Many, however, are quite small, only a few square yards in area and a few cubic yards in volume, like many of the small ones on cleared ground. If rainforest trees were as effective in holding the soil as is usually believed, one would think they should have restrained such slides as these.

It is therefore perfectly clear that landslides are normal for this kind of topography even under rainforest. This conclusion does not prove, however, that the slumps of 1950 and 1951, which are so evident on cleared ground, would have occurred if the forest cover had not been removed. It is possible that the conditions that caused slumping in grassland in 1950 and 1951 were not the kind of conditions that cause slumping in rainforest. To prove that removal of vegetation had no effect it would be necessary to demonstrate, first, that slumps occurred under rainforest in 1950 and 1951, and secondly, that they occurred as frequently as on comparable cleared ground.

The first point can be established beyond reasonable doubt. Three slumps have been found on the Maleny Plateau, two in rainforest and the other in *Tristania-Eucalyptus* forest, the scarps of which are so bare and steep, so little colonized by vegetation, that they are almost certainly contemporaneous with the slumps in cleared pasture nearby. One of the rainforest slumps is on an average slope of only 19° (Fig. 6); the other is where slope changes from 25° above the break to 19° below it—surely an unusual position. The third slump is in the steep head of a small drainage, on a slope of probably between 35° and 40° origi-

nally. There seems to be no essential difference in character, therefore, between slumps in forest and pasture, and exceptionally wet weather evidently promotes them under both kinds of cover.

FIG. 6.—A fresh slump scarp under rainforest. Vertical displacement here is 28 inches, lateral displacement about 20 inches. This scarp is at least 150 feet long, varies in height, and breaks into several smaller scarps in some places. In one portion trees have been overthrown and a jungle of shrubs and vines is rapidly growing up. Average slope 19° northeast. Scale is marked in inches. Maleny Plateau, March 25, 1952.

We have not yet encountered evidence of semiliquid flow on low gradients under rainforest, however, although these are common in pasture.

The second point, that slumps are equally common under rainforest, is by no means established. Our sample of rainforest is small in comparison with the area of cleared pasture that may be seen with equal effort; consequently fewer slumps may simply reflect a smaller sample.

The differing character of ground surface under the two types of cover complicates the question. Under rainforest there is little vegetation on the surface—some tree reproduction but scarcely any grasses, forbs, or undershrubs. The thicker the canopy above, the less vegetation below. Litter cover, considering luxuriance of the canopy, is remarkably scanty: fresh-looking leaves and twigs, obviously newly fallen, lie upon so thin a decomposing layer as to be almost directly upon mineral soil (Fig. 7). In many places, surface soil is exposed, often by no more than the scratching of small birds. Processes of decay in this damp, subtropical environment are so rapid that there is no opportunity for the development of a thick and continuous carpet of duff such as one finds in many temperate forests.

In contrast to the scanty ground cover in rainforest, the surface soil of pasture is covered with a tight sod of herbaceous vegetation (Fig. 8).

It is quite clear that superficial movement of

FIG. 7.—Thin litter and exposed bare soil under rainforest, Mt. Glorious. Note accumulation above root or surface, lower left. Matchbox is 2-¼ x 1-⅝ inches April 10, 1952.

FIG. 8.—Paspalum turf on a 20° westerly slope, Maleny Plateau. A dense sod holds the surface firmly. The grass is exceptionally short because this area has been heavily grazed. Scale is marked in inches. April 16, 1952.

soil—landslides excluded—is much more rapid under rainforest than under pasture such as this. The soil under rainforest is loose and rocky, and on steep slopes when dry or moist it may slide readily underfoot and roll downhill. Even the scratching of birds and other small animals causes noticeable displacement in this way. Exposed soil surfaces reveal evidence of wash both from leafdrip and stemflow. Less direct but more impressive evidence of rapid downward movement is provided by accumulations of earth and rock above fallen logs, since wood decays quickly under rainforest. The banks so formed crumble downhill after the logs have rotted. Accumulations also take place above the bases of standing trees, only to crumble or slump into the cavity created when the tree is overthrown or the stump decays (Figs. 9, 10). In some places one can

trace a series of small slumps above a windthrow cavity, representing successive adjustments of slope to removal of support. In consequence of these movements and temporary restraints, the surface of the forest floor is rough, a surface of humps and hollows. Many of these indications of downslope movement are small individually but, since they are general over the entire slope, aggregate mantle movement in even so short a time as 50 or 100 years must be very considerable. Penck (1924) emphasizes the temporariness of restraint imposed by forest roots on movement of the mantle.

FIG. 9.—An accumulation of perhaps 1-½ cu. yd. of soil and rock above a stump; this will slide into the cavity as the stump decays. Considerable soil was also carried down by the fallen bole on ground at left. Note basal curvature of stem at left, suggesting instability when the tree was small. Tangle of undergrowth is a response to opening of the canopy. Average slope 25°. National Park, Mapleton. March 14, 1952.

FIG. 10.—Cavity created by windthrow; the roots of the fallen tree can be seen at right. Soil and rock from above are now sloughing into the cavity, and a considerable volume has been carried downward by the tree roots. Note rockiness of slope and characteristic scarcity of ground vegetation. Average slope 35° west. Near Grevillea, N.S.W. March 7, 1952.

A still less direct but nonetheless important evidence of rapid mantle movement is the rockiness of practically all these slope soils in an environment provocative of rapid chemical weathering. The rocks may be derived from major slumps which play so dominant a part in shaping this topography, but their distribution over the length of the slopes is doubtless aided by the smaller movements that have been described.

Another indirect indicator of instability is curvature of tree trunks (Fig. 11). This curvature is obviously related to direction and steepness of slope: it is prevailingly convex downslope, no matter what the exposure may be, and is most marked on slopes that are steep. Curvature is explained by tilting the stem because of mantle instability, followed by upward growth of the stem tip.

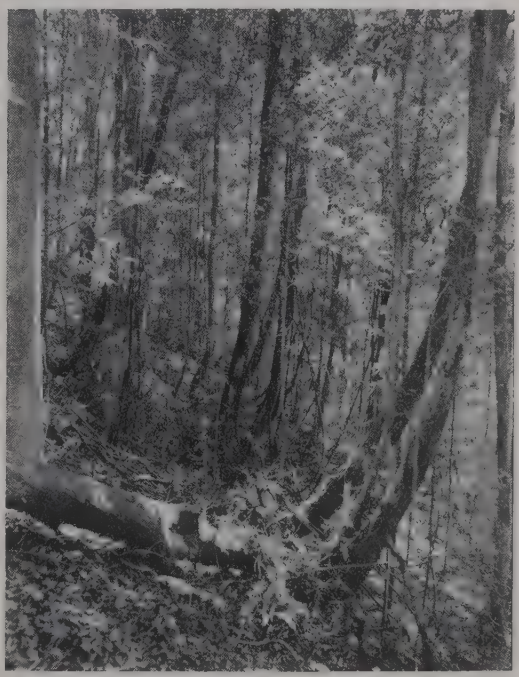

FIG. 11.—Trunk curvature in rainforest, Maleny Plateau. It is believed that mantle instability, either gradual creep or abrupt slips, tipped some of the stems, which have grown vertically since. Because curvature is most common in the basal part of the stem (right), the distorting effect of instability is presumed to be greatest when the tree is small; however some stems were evidently tipped when fairly large (left middle distance). Note characteristic absence of herbaceous vegetation. Average slope 32° northeast. Scale is marked in inches. March 25, 1952.

The distribution of curvature suggests that mantle movement at a given spot is intermittent rather than continuous. Not all trees exhibit curvature, even in a fairly uniform stand. Fur-

thermore, curvature is not continuous throughout the length of the trunk, commonly being most marked in the lower one-third or less. While movement over a whole slope is presumed to be more or less continuous, its distorting effect is apparently greatest while the tree is small, but becomes reduced when the tree is a larger and more effective impediment. Some cases of curvature could result from pressure by a downward-moving object, such as a stone, when the tree was small.

Evidence of superficial movement in grassed pasture—again, ruling out landslides—is very much less than under rainforest. The only evidence of wash is in heavily used cowtrails. In places where cows are forced to concentrate, severe gully erosion may result. General superficial movement, however, the sliding, rolling, and washing so common on steep forested slopes, is practically absent on paspalum or kikuyu grass pasture. The surface of pasture is smoother than the soil surface under rainforest; these smoother contours are partly an illusion created by the mantling carpet of grass, but they are partly a result of the filling in of irregularities of the forest-soil surface after felling and burning.

The evidence may be summed up as follows: Slumps occur under both rainforest and pasture. Various kinds of soil movement take place in rainforest that do not occur in pasture. If slumps are less frequent under rainforest than in pasture, as is generally believed, these other kinds of movement lessen the difference in total displacement.

Discussion

What happens when slopes are cleared of rainforest and sown to pasture? When the trees are felled and burned, and before a sod is established, considerable sliding and rolling takes place so that there is a new adjustment of mantle to slope. Minor adjustments doubtless continue for a time as unburned tree roots decay beneath the grass sod, but these are not readily visible.

A difference created by clearing, which probably has a bearing on soil stability, is in burden of vegetation. A rainforest burden of some hundreds of tons per acre, very unequally distributed, is replaced by a few tons of grass per acre distributed uniformly. There is no reason to think that the greater weight of forest vegetation favors or hinders landslides (Hacker 1940), but the uneven distribution of weight and the release that occurs when a tree decays or is overthrown may be important in encouraging the kinds of soil movement we have noted under rainforest. Doubtless this release is reflected in some of the sliding and rolling that takes place when the forest is cleared.

The climatic stratum controlled by vegetation shrinks upon clearing from a depth of 100 feet to a few inches. Although this makes an impressive difference in light, heat, wind, and humidity at the level in which a human being moves, the difference is not so great at the surface of the ground under thick grass. Extremes of temperature and moisture are possibly greater under grass, and it may be that during periods of drought, the soil of grassland dries and cracks more than under rainforest. Soil moisture is also influenced by difference in consumption of water by the two kinds of vegetation, but what the difference may be is not known.

Possibly some of the factors incidental to clearing magnify the action of internal components of creep in the mantle. Greater variation between high and low temperatures (though temperatures in southeastern Queensland are seldom low enough to freeze even the surface of the soil), and possibly greater drying of surface soil under grass should assist creep by the settling downhill that takes place as the mantle alternately swells and shrinks. Trampling by livestock may also intensify creep in grassland. On the other hand, growth and decay of tree roots would seem more conducive to creep than growth and decay of grass roots, but this might not be so if the annual change in volume of roots is greater under grass than under forest. Quantitative displacement by these internal factors of creep is not easy to appraise, but certainly, in comparison with the obvious displacements by slope wash, sliding, and rolling that are observed under rainforest, they are not very great.

Although the soil is occupied by different kinds of roots under the two kinds of cover—thick, woody roots being absent, of course, under grass—the two root systems occur through about the same depth of soil. Most roots, both of rainforest trees and of grasses, are concentrated in the surface foot, with a few penetrating to two feet, and very few indeed—and these on deep red soils of the plateau top rather than on the less permeable slope soils with which we are concerned—going as deep as three feet. This fact suggests that the physical effects of roots and depletion of soil water under the two kinds of vegetation are confined to the same zone.

The notion that rainforest roots stabilize the mantle on slopes is only partly true. Roots do provide stability during the life of the tree: this is indicated by the character of stem curvature, by the way in which soil and rock are bound in roots that have been exposed, and by the accumulation of soil materials above the base of the tree. This stability, however, is only temporary: when the

tree dies and its roots decay, the mantle readjusts to new conditions of support and load and a material displacement goes on downhill. The fact that roots of most rainforest trees are superficial suggests that they do little to bind the lower part of the mantle. They do not appear to give the anchorage in fissures of bedrock, for example, that is provided in deeper-rooted eucalypt forest. In contrast to the manifest instability of the mantle under rainforest, a grass sod forms a very stable surface indeed—except when it is broken by landslides.

It seems probable that differences in disposal of rainfall by forest and by pasture may have more to do with the incidence of landslides than differences in the binding effects of their roots. The association of landslides in 1950-51 with prolonged, heavy rainfall indicates that a highly essential factor is the building up of a large volume of water in the mantle. This being so, that type of vegetation should be the more effective in preventing landslides which more reduces the amount of water in the mantle by promoting either overland flow, seepage to low-lying aquifers, or evapotranspiration.

We know little, by direct observation in the two types of cover during storms, of the likelihood of overland flow—or, conversely, of the rapidity with which water soaks into the soil, under either. If the treading of livestock generates slip planes, as suggested by Sharpe (1938), or if grass improves the structure of surface soil so as to permit more rapid infiltration and hence more frequent saturation, clearing and pasturing may increase the likelihood of landslides. On the other hand, if treading makes the soil more compact and produces a platy structure near the surface, as reported for heavily grazed pasture in Pennsylvania by Robinson and Alderfer (1952), clearing and pasturing may encourage overland flow and thus lessen the likelihood of prolonged saturation and landslides. The best way to answer such questions is to observe the behaviour of the water during prolonged and heavy rains, supplementing such observations with measurements of moisture penetration in the soil. An experimental attack through the use of infiltrometers (rainfall simulators) might yield at least part of the necessary information.

If differences should be demonstrated in the amount of overland flow under rainforest as compared with pasture, an explanation would probably require study of seepage through the mantle and into lower-lying aquifers. It has been pointed out that the root systems of both the trees and the grass occupy the same general level, but the coarseness of the one and the fineness of the other, together with their effects on soil structure, may well influence percolation differently throughout the mantle, and this may have an important bearing on the rapidity of subterranean flow. The possibility of such differences and the likelihood of their bearing on the problem could be explored by measuring moisture penetration under the two types of vegetation during and immediately following storms capable of causing overland flow, or in connection with infiltrometer trials.

If evapo-transpirational losses from the two kinds of cover were greatly different, this might explain differences in the disposal of rainwater during storms. Supposing that one type of vegetation depleted the soil moisture more than the other, it follows that a greater storage capacity is created, the mantle is less likely to be saturated by the next rain (or it will be saturated for a shorter time), and therefore it is less likely to slip. We know nothing of the magnitude of evapo-transpirational losses by rainforest or pasture. Their application to the problem at hand can be most easily attacked, probably, by measuring trends in soil moisture under the two types of cover. As has been suggested already, such measurements would also give an insight into possible differences in infiltration and seepage flow.

Summary and Conclusions

Numerous landslides occurred on the flanks of steep-sided plateaus in southeastern Queensland in 1950 and 1951. These slopes, which formerly supported subtropical rainforest, have been cleared and sown to pasture. The Maleny Plateau, about 50 miles airline north of Brisbane, and 1,500 feet above sea level, is used as an example. Here average annual precipitation is about 74 inches. During February and July 1950 and January 1951 precipitation was exceptionally high, and on certain days during the periods of prolonged rainfall from 4 to as much as 12 inches fell. It is believed that the landslides were associated with these heavy falls when the mantle was saturated for long periods, Slumping is believed to have been favored also by the character of the slope soil, a dark brown solum about 18 inches deep overlying a deeply weathered but rather impermeable clay subsoil that probably promoted lateral flow of water in the upper part of the mantle.

Observations of mantle movement in cleared pasture and under rainforest were made in a number of localities in the summer of 1951-52. Slump scarps of many sizes and ages were found on steep slopes within rainforest, and it is clear from these observations and from aerial photos that slumping is a normal geomorphic process here. Slumps

were found in rainforest which appeared to be contemporaneous with recent slumps in cleared pasture, but because the rainforest sample was small compared with extensive areas of cleared pasture on which slumping could be seen, it could not be determined whether the frequency of occurrence of slumping in rainforest was in fact different from that in pasture.

On steep slopes under rainforest, mantle movement is normally rapid. This is revealed not only by the readiness with which soil is displaced underfoot, but by such evidence as its rockiness in an environment where rock decay is probably rapid, by accumulations of soil and rock above trees and down logs, by sloughing into cavities created by overthrow or decay of trees, and by downslope curvature of tree trunks. Under rainforest there is little undergrowth and very little litter on the soil surface; the litter is readily displaced by such slight disturbances as the scatching of birds, exposing the soil to erosion by leaf drip and stemflow. In contrast, there is little superficial movement in most pasture; the soil is firm underfoot and the surface is closely covered and tightly held by the grass sod.

It is concluded that landslides are not wholly a new phenomenon caused by clearing rainforest. Some landslides occurred before the forest was felled; some still occur in rainforest. Others may be a result of forest clearing, but if they are, the reason is not the one commonly given—that landslides occur because the restraint imposed by tree roots is removed. The restraint imposed by tree roots appears to be a rather minor factor in causing whatever differences there may be in the frequency of occurrence of landslides under rainforest as compared with pasture. Such differences are more probably attributable to differences in disposal of rainwater under the two types of cover.

Soil movement other than landslides is very rapid on steep slopes under rainforest, and possibly some of the slumps and flows under pasture are but a different expression of this normal, more or less continual, mantle movement. A sod of grasses ordinarily holds the surface soil more firmly and completely than roots of forest trees, yet abundant slumps and flows demonstrate that such sod cannot cope with the tensions that build up during prolonged periods of very wet weather. In evaluating the effects of forest clearing, different kinds of mantle movement must therefore be evaluated; whether total displacement over the years is greater under pasture or under rainforest is not now known. An answer to this question and an understanding of the factors furthering or retarding movement cannot be reached until more detailed studies are made.

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MORTALITY RATES OF WHITEFISH IN AN ARCTIC LAKE[1]

Donald E. Wohlschlag
Natural History Museum, Stanford University, California

Introduction

A knowledge of mortality rates, coupled with a knowledge of growth rates and population density, is essential as a basis of studies on biological production rates—studies which are fundamental to an understanding of both theoretical and applied population ecology. Although growth-rate data and population estimates or censuses can be made available for animal populations with relative ease, mortality rates are especially difficult to obtain and evaluate. Neave (1953) has emphasized the particular importance of determining and understanding changes in types and magnitudes of mortality rates with the stages of growth of individuals in salmon populations. Unfortunately the methods of estimating mortality rates in salmon populations are not altogether applicable to non-migratory fish populations. Up to the present, mortality rate determinations in non-migratory fish populations have been made by methods of following the abundance of a given group of marked fish over specified periods of time (Jackson 1939), by catch-curve methods (Baranov 1918), and by methods of relating mortality from fishing to the fishing effort (Silliman

[1] These studies were aided by a contract between the Office of Naval Research and Stanford University, contract number Nonr-225(08).

1943). These methods have been discussed in detail by Ricker (1948).

From certain theoretical considerations, at least, the fish of arctic lakes should provide ideal experimental populations inasmuch as complications associated with exploitation, with high growth and recruitment rates, and with high mortality rates would be minimized. Accordingly, the purpose of this paper is to discuss several aspects of the mortality rates to which two species of whitefish are subjected in Ikroavik Lake near Point Barrow, Alaska. In this roughly oval-shaped lake with a long axis of about two and one-half miles and with a maximum depth of about seven and one-half feet, there have been estimated to be approximately 5,700 *Leucichthys sardinella* and 200 *Coregonus nasus* having fork lengths over 180 millimeters; no piscivorous species were found (Wohlschlag 1953). Since the ice freezes to a depth of about six feet, a question arose as to the extent of the winter mortality of the populations in their restricted winter environment. Though there was no direct evidence to indicate that excessive population losses due to natural mortality or emigration occurred during the two-month ice-free season when population estimates were being made by the Schnabel (1938) mark-and-recapture method, it was necessary to know definitely whether the losses were small enough for the estimates to be valid. In this connection, it was considered desirable to investigate the attractive possibilities of utilizing the same capture-recapture data for a determination of the summertime mortality rates by methods recently described by Leslie and Chitty (1951) and by Bailey (1951). Comparisons of the summertime morality rates estimated by the two methods with the annual rates determined from survivorship (age-frequency) data of Cohen (1953) were then made for the purpose of discovering whether any gross changes of mortality rates occurred within the year.

The help and advice of Dr. Ira L. Wiggins, Director of the Arctic Research Laboratory at Point Barrow, and his staff were indispensable for the successful accomplishment of the field work for this study. Other investigators generously cooperated to make transportation facilities available for the field operations. Special thanks are extended to Mr. Daniel M. Cohen, Project Assistant, for his aid in the field work and in processing the data. Grateful acknowledgment is accorded Dr. W. E. Ricker, Fisheries Research Board of Canada, and Mr. T. M. Widrig, U. S. Fish and Wildlife Service, who critically reviewed the manuscript.

Procedure

From July 15 through August, 1952, the two species of whitefish were sampled in Ikroavik Lake with a 200-foot tapered seine having ¾-inch bar mesh. In August additional fish were sampled with a 100-foot, 1-inch bar mesh gill net. A September 3-10 sampling was carried out with this 100-foot gill net and two "experimental" gill nets. Each experimental gill net was comprised of five 50-foot sections having ¾-inch, 1-inch, 1-¼ inch, 1-½ inch, and 2-inch bar meshes, respectively.

To obtain some idea of the fraction of fish which died each year, the catch-curve technique based on age-class composition as described by Ricker (1948) was utilized. The information on age-class composition was taken from the data prepared by Cohen (1953).

Mark-and-recapture observations on *Coregonus nasus* were begun on July 15, 1952 and continued until September 10, 1952, while *Leucichthys sardinella* observations lasted from July 31 until September 10. On July 15, ten *C. nasus* were marked with numbered Petersen discs. During the remainder of July both species were marked with a clipped adipose fin; during each week of August a different paired fin was clipped. Only the tips of the paired fins were clipped and extreme care was exercised in handling the fish from the time of capture until they were released near the center of the lake. Records were kept of the numbers of recaptures bearing one or more one or more marks, the numbers of unmarked fish which appeared in each sample, and the numbers which were marked and released during each sampling. Only fish whose fork lengths were 180 millimeters or over were considered in the sampling operations. The capture-recapture data for the estimation of survival (and mortality) rates were tabulated by combining the various classes of marks by the Leslie and Chitty (1951) "Method B".

Leslie-Chitty Method B

From an unknown but "closed" population consisting initially of N_0 fish at time $t = 0$, let R_0, R_1, R_2, . . . , R_T be the number of individuals randomly sampled at equispaced time intervals t ($t = 0, 1, 2, \ldots, T$). At any time t the sampled individuals are characteristically marked and released at random into the environment. Among the R_t sampled, u_t would be unmarked and s_t would appear with one or more marks. Without loss of information, the separate classes of marks may be combined so that m_{xt} is the number of individuals which are sampled at time t and which were last captured at time x ($x = 0, 1, 2, \ldots, T - 1$) so that $\Sigma\, m_{xt} = s_t$. If C represents a

constant survival rate from t to $t+1$, the population would decrease between sampling intervals from N_t to N_tC assuming that both marked and unmarked fish die at the same rate and that both are equally vulnerable to the sampling gear. Starting operations with $R_0 = u_0$ at t_0, the following deterministic schedule of expected and observed results can be set up for periods to $t = 3$.

Classes of marks x	Sampling Intervals							
	$t=0$		$t=1$		$t=2$		$t=3$	
	Expected marks at large	Number of marks observed	Expected marks at large	Number of marks observed	Expected marks at large	Number of marks observed	Expected marks at large	Number of marks observed
0	...	...	R_0C	m_{01}	$R_0C^2-m_{01}C$	m_{02}	$R_0C^3-m_{01}C^2-m_{02}C$	m_{03}
1	...	...	...	...	R_1C	m_{12}	$R_1C^2-m_{12}C$	m_{13}
2	...	...	...	...	.....	...	R_2C	m_{23}
Total expected marks at large and number observed with marks (s_t)	...	...	R_0C	s_1	$R_1C^2+u_1C$	s_2	$R_0C^3+u_1C^2+u_2C$	s_3
Number unmarked (u_t)	u_0		u_1		u_2		u_3	
Number marked and released (R_t)	R_0		R_1		R_2		R_3	

For "three-point" sampling, *i.e.*, where $t = 0$, 1, and 2, the maximum likelihood formula for the estimated survival rate, $\hat{C}$, from the above schedule is

$$\hat{C} = \frac{s_2\, m_{01} + u_1\, m_{02}}{R_0\, m_{12}} . \qquad (1)$$

The variance of the estimate is

$$V(\hat{C}) = \frac{m_{02}\, s_2\, R_1^2}{m_{12}^3\, R_0^2} , \qquad (2)$$

and the standard error would be the square root of this value. For four-point sampling the appropriate relationship, which can best be solved by iterative methods, is

$$\frac{m_{02}\, R_0}{R_0C - m_{01}} + \frac{m_{03}(2R_0C - m_{01})}{R_0C^2 - m_{01}C - m_{02}} + \frac{m_{13}R_1}{R_1C - m_{12}} = \frac{s_2R_0}{R_0C + u_1} + \frac{s_3(2R_0 - u_1)}{R_0C^2 + u_1C + u_2} . \qquad (3)$$

For five-point sampling, not considered in this study, the formula given by Leslie and Chitty would be appropriate. Their suggested iterative method of solving the five-point equation could be applied to the four-point equation above.

The use of the Leslie-Chitty Method B has the advantage that removals of marked and unmarked individuals by accidental deaths or by deaths due to exploitation can be accounted for very simply when there are D_t deaths known for each time interval in which the total catch is F_t. In these circumstances the formulas given above hold but $R_t = F_t - D_t$ applies only to live fish which are marked and released, and u_t unmarked fish in each sampling interval can be corrected for deaths by letting $y_t = u_t - D_t$ and by substituting y_t for u_t. The effect of the D_t deaths is, of course, to lower the existing survival rate.

The fraction of the population which dies during each time interval is Q, or the complement of C; thus

$$Q = 1 - C.$$

The fraction, Q, could be broken up into natural and fishing mortality components in instances where fishing with a known rate of exploitation occurred. For comparative purposes, the instantaneous rate of mortality, i, can be computed on a daily basis from the relationship, $C = e^{-iT}$ or $i = (-\log_e C)/T$, where e is the natural logarithmic base and T is the time in days over which the survival rate, C, has been calculated. These methods of application of mortality rates have been summarized by Ricker (1944, 1948) and by Deevey (1947).

"Triple-Catch" Trellis Method

Data which are tabulated as in the above schedule can also be treated by the trellis-array technique used successfully by Dowdeswell, Fisher, and Ford (1940, 1949) and by Fisher and Ford (1947). The generalized solutions for population size, death rates, and birth rates from triple-catch arrays have been given by Bailey (1951). For large samples, the survival rate over the respective periods of time T_1 days between $t = 0$ to $t = 1$ and T_2 days between $t = 1$ to $t = 2$ is

$$\hat{C} = e^{-\hat{i}T_1} = u_1\, m_{02}/u_0\, m_{12}. \qquad (4)$$

The large-sample variance of $\hat{C}$ is

$$V(\hat{C}) = C^2\,(1/m_{12} + 1/m_{02}), \qquad (5)$$

and the large-sample variance of $\hat{i}$ is

$$V(\hat{i}) = 1/m_{12} + 1/m_{02})/T_1^2. \qquad (6)$$

Bailey has also given approximately unbiased formulas applicable to small-scale sampling when m_{01}, m_{02}, and m_{12} are small. The corresponding estimates are approximately

$$\check{C} = e^{-\check{i}T_1} = u_1 m_{02}/u_0(m_{12}+1), \quad (7)$$

and

$$V(\check{C}) = C^2 - \frac{u_1^2 m_{02}(m_{02}-1)}{u_0^2 (m_{12}-1)(m_{12}-2)}. \quad (8)$$

Various estimates for population size and birth rate given by Bailey and other authors will not be considered in this paper.

Results and Calculations

Leslie-Chitty Method

The three-point capture-recapture data for *Leucichthys sardinella* and *Coregonus nasus* are summarized in Tables I and II, respectively.

Table I. *Three-point capture-recapture data for estimation of 21-day survival rate of Ikroavik Lake* Leucichthys sardinella *in 1952. (See text for explanation of symbols.)*

Classes of recaptures* x	Number of recaptures m bearing different marks during intervals t=0, 1, 2		
	t=0 July 17 to Aug. 6. Mid-date July 27	t=1 Aug. 7 to Aug. 27. Mid-date Aug. 17	t=2 Aug. 28 to Sept. 17. Mid-date Sept. 7
0	0	1	5
1	..	..	12
Recaptures in sample s_t	0	1	17
No. unmarked in sample y_t	96	194	355
Total number sampled R_t	96	195	372
Number removed D_t	19	31	...
Total catch F_t	115	226	...

*In class x=0 adipose and left ventral fin clips were used. In class x=1 right ventral, left pectoral, and right pectoral fin clips were used.

Upon substitution into the maximum likelihood formula (1), the *L. sardinella* data yield the following survival rate on the basis of three 21-day intervals:

$$\hat{C} = \frac{(17)(1)+(194)(5)}{(96)(12)} = 0.86,$$

with an instantaneous death rate $\hat{i}$ on a daily basis equal to 0.0072, and with a standard error of $\hat{C}$ from the square root of (2) equal to

$$\sqrt{\frac{(5)(17)\times(195)^2}{(12)^3\times(96)^2}} = 0.45.$$

Table II. *Three-point capture-recapture data for estimation of 28-day survival rate of Ikroavik Lake* Coregonus nasus *in 1952. (See text for explanation of symbols.)*

Classes of recaptures* x	Number of recaptures m bearing different marks during intervals t=0, 1, 2		
	t=0 July 3 to July 30 Mid-date July 16-17	t=1 July 31 to Aug. 27 Mid-date Aug. 13-14	t=2 Aug. 28 to Sept. 24. Mid-date Sept. 10-11
0	0	3	1
1	..	..	5
Recaptures in sample s_t	0	3	6
No. unmarked in sample y_t	10	22	25
Total number sampled R_t	10	25	31
Number removed D_t	2	1	..
Total catch F_t	12	26	..

*In class x=0 Petersen discs plus adipose fin clips were used. In class x=1 adipose, left ventral, right ventral, left pectoral, and right pectoral fin clips were used.

In a similar manner, for three 28-day intervals, the survival rate for *C. nasus* from (1) is $\hat{C}$ = 0.80, with an instantaneous death rate $\hat{i}$ on a daily basis of 0.0079, and with a standard error of $\hat{C}$ from (2) equal to 0.55.

The 21-day mortality rate for *L. sardinella* would be 0.14; the 28-day mortality rate for *C. nasus* would be 0.20.

The capture-recapture data were also treated by groupings of three and four successive 14-day intervals, but in all cases too few recaptures were available to allow satisfactory estimates. Particular difficulty due to lack of recaptures in four-point estimation from (3) arose when such terms as m_{02}, m_{03}, or m_{13} equalled zero so that entire terms of the four-point equation disappeared.

Triple-Catch Method

For *Leucichthys sardinella*, the large-sample estimate of the 21-day survival rate from (4) is

$$\hat{C} = (194)(5)/(96)(12) = 0.84,$$

with a corresponding daily instantaneous death rate of 0.0083. The large sample standard errors from formulas (5) and (6), respectively, are

$$\sqrt{V(\hat{C})} = \sqrt{\left\{\frac{(94)(5)}{(96)(12)}\right\}^2 \left\{\frac{1}{12}+\frac{1}{5}\right\}} = 0.45$$

and

$$\sqrt{V(\hat{i})} = \sqrt{(1/12+1/5)/(21)^2} = 0.0253.$$

The small-sample approximation of the survival rate for the *L. sardinella* data from (7) is

$$\check{C} = (194)(5)/(96)(12+1) = 0.78,$$

with a corresponding daily instantaneous mortality rate of 0.0118. The small-sample standard error of $\check{C}$ from (8) is approximately

$$\sqrt{V(\check{C})} = \sqrt{\left\{\frac{(194)(5)}{(96)(12+1)}\right\}^2 - \frac{(194)^2(5)(5-1)}{(96)^2(12+1)(12+2)}} = 0.39.$$

For *Coregonus nasus,* the large-sample estimate of the survival rate from (4) is $\hat{C} = 0.44$, which corresponds to a daily instantaneous death rate of 0.0257. The large-sample standard errors from formulas (5) and (6), respectively, are $\sqrt{V(\hat{C})} = 0.482$, and $\sqrt{V(\hat{i})} = 0.0391$. The small-sample approximation for the *C. nasus* survival rate from (7) is $\check{C} = 0.37$, with an appropriate daily instaneous mortality rate of 0.03579. The small-sample standard error of $\check{C}$ cannot be computed adequately since the second term of equation (8) disappears; thus $\sqrt{V(\check{C})} = \check{C}$. Obviously the above triple-catch equations yield totally unsatisfactory results with the too-limited *C. nasus* data; the results are given only because they illustrate the effects of inadequate field capture-recapture operations.

Age-Frequency Data

The age-frequency data for *Leucichthys sardinella,* based on age determinations from scales of 1,084 specimens, are given in Table III in which the annual and daily expectations of death have been computed from the annual instantaneous rates of mortality. For comparative purposes the calculation of the daily expectations of death is predicated on the assumption that mortality is constant throughout the year. The annual instantaneous rates have been computed from the differences between the natural logarithms of the frequencies at successive ages from the age of five. This procedure has been described by Ricker (1944, 1948). The logarithms of the frequencies are plotted against the ages in Figure 1. The frequency polygon drawn between ages five and eleven indicates the possibility of age-specific mortality, especially since a fairly "smooth" catch-curve seems to exist for this range of ages. If no age-specific mortality be admitted, the broken straight line plotted for the same age range would be appropriate. The least-squares equation of this line has a slope of −0.889 which is an average annual instantaneous rate; the corresponding daily expectation of death, d, is

$$d = 1 - e^{-0.889/365} = 0.0027.$$

(Note that the expectation of death d is approximately equal to the negative exponent of the logarithmic base e when the exponent is small.) The frequencies of two-, three-, and four-year-old fish are not representative of the true abundance of the fish, since fish of these age groups were too small to be fully vulnerable to the gear. Over

TABLE III. *Age-frequency data for catches of Ikroavik Lake* Leucichthys sardinella *with calculated annual and average daily death rates*

Age	Frequency (f)	$\log_e f$	Annual instantaneous death rate (i)	Annual expectation of death* (a)	Average daily expectation of death† (d)
0	0	.....	.....	.....	.....
1	0	.....	.....	.....	.....
2	32	3.46574	.....	.....	.....
3	527	6.26720	.....	.....	.....
4	74	4.30407	.....	.....	.....
5	164	5.09987	0.19460	0.18	0.0005
6	135	4.90527	0.43936	0.36	0.0012
7	87	4.46591	0.57409	0.44	0.0016
8	49	3.89182	1.40691	0.75	0.0038
9	12	2.48491	1.38630	0.75	0.0038
10	3	1.09861	1.09861	0.67	0.0030
11	1	0.00000			

*$a = 1 - e^{-i}$, where e is the natural logarithmic base.
†$d = 1 - e^{-i/365}$.

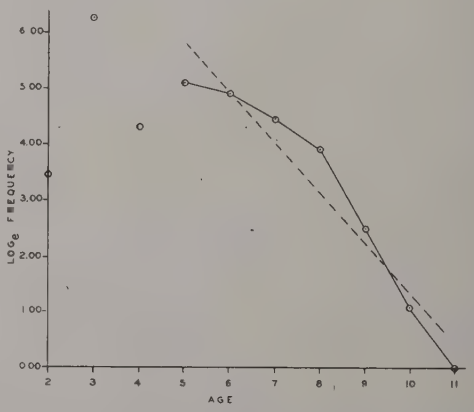

FIG. 1. Natural logarithms of the frequencies plotted against the ages of *Leucichthys sardinella* taken during 1952 in Ikroavik Lake. Broken line calculated by least-squares method for data from ages five to eleven.

half the two- and three-year-old fish were fortuitously retained in a single seine haul, and some of the four-year-old fish were considerably shorter than the 180 millimeter fork length minimum so that they could have escaped through the smallest-meshed gear used.

Unfortunately, the meager sample of 73 *Coregonus nasus* did not provide sufficient information for the estimation of annual mortality rates, but the data did indicate that there had been pronounced fluctuations in mortality, or recruitment, or both.

Discussion

The Leslie-Chitty, the triple-catch trellis, and the age-frequency procedures for the estimation of mortality rates depend on random sampling. Samples from the seine hauls and from the gill netting were quite similar with respect to length-frequency and age-frequency distributions of fish whose fork lengths were over 180 millimeters so that all fish above this length were considered to be fully vulnerable to the gear. Also it may be concluded that neither species experienced significant recruitment due to growth of fish into the 180-millimeter range during the study, since this minimum length coincided with a break in the length-frequency distribution of the *Leucichthys sardinella* occurring between the ages of three and four, and since this minimum excluded only a very few *Coregonus nasus* among those sampled. (It should be noted that some four-year-old *L. sardinella* had fork lengths less than 180 millimeters.) The difficulties of sampling from schooling aggregations were ameliorated by sampling over fairly long periods of time (Wohlschlag 1953).

Because the use of the capture-recapture techniques holds much promise for application to field ecological studies of animal populations, some of the fundamental assumptions of the techniques, other than those discussed in the preceeding description, will be given. Leslie and Chitty (1951) have pointed out that their method generally applies to a series of samples taken from a large population where risk of recapture of marked individuals is small. If, in smaller populations, the risk of recapture becomes great, formulas developed on the basis of hypergeometric distributions of marked and unmarked individuals would be more appropriate. However, in fish populations—even with intensive sampling of small natural populations—the fraction of all the fish likely to be sampled is small (Tables I and II) so that the formulas derived from multinomial distributions are full adequate. The large-sample formulas as given by Leslie and Chitty (1951) and by Bailey (1951) have been derived from a consideration of deterministic models in which the survival rate has been regarded as a *constant* rather than as a *probability* which would result from a consideration of stochastic (probabilistic) models. It should also be emphasized that the deterministic models above consider that death rates fall equally on all age-classes under consideration.

Later studies of Leslie (1952) and Leslie, Chitty, and Chitty (1953) have confirmed the utility of the deterministic formulas for reasonably large-scale sampling. Moran (1952) has evaluated the Leslie-Chitty formulas and concludes that they are fully efficient under the assumptions of the deterministic model; and, although he has noted that probabilistic models might be more appropriate, he has not investigated their solutions. In general, for small, non-homogeneously mixed groups, stochastic processes are better than deterministic methods for the estimation of population parameters (Bailey 1953). Unfortunately, the probabilistic capture-recapture models remain to be constructed and solved for the estimation of survival or mortality rates.

The estimates of the death-rate parameter by the various formulas of Bailey (1951) take into account the "birth rate" which would correspond to recruitment at the 180-millimeter fork length in this study. Since the recruitment at this size was small due to the fact that there appeared in the initial samples relatively few fish which were slightly below 180 millimeters and which would have grown into the 180-millimeter range during the study, recruitment would have caused only negligible bias in the death-rate estimates. Bailey has developed his formulas by assuming that the birth date is proportional to population size; to extend the assumption that recruitment at 180 millimeters (for fish four and five years old) is proportional to the population size would be somewhat hazardous. A comparison of large-sample formulas (1) and (4) in the absence of recruitment reveals immediately that more information is used in formula (1). Even so, the survival rate estimates and their standard errors in these two cases are approximately the same for the *Leucichthys sardinella* data.

Because it is obvious that both whitefish species were studied on the basis of small samples, small-sample formulas such as (7) would adjust the data to yield an approximately unbiased estimate of the survival rate. Encouragingly enough, the *L. sardinella* daily death rate estimate from small-sample formula (7) is of the same order as those from large-sample formulas (1) and (4). Nev-

ertheless the standard errors of all these estimates are very large, so that sampling would ordinarily have to be conducted on a much larger scale if relatively small standard errors were to be expected. Particularly unsatisfactory are the all-too-meager sample data for *Corgegonus nasus*, but it is instructive to compare the survival rate estimates from the various formulas to note the effect of the presence or absence of a single recapture and the effects of the different formulas, keeping in mind that the survival rate estimates except possibly from (1) are unreasonably low.

For many animal populations in the field, only very small fractions can be obtained and given characteristic marks. For this reason some method of grouping the marks would ordinarily be necessary. Leslie and Chitty have noted that their Method B of grouping the data (also used in this study) is "efficient" because no information is lost. When there is no *a priori* information on population size or the fraction sampled, grouping the data could best be accomplished if the marks were changed at small time intervals; better yet would be the use of consecutively numbered tags. Then the length of the time interval necessary to secure a fair representation of different classes of marks could be determined by combining the small time intervals into larger ones after the study has been undertaken. An interesting possibility of improving the technique by sampling until there are fixed numbers of variously marked individuals (inverse sampling) remains to be investigated. Also uninvestigated are the properties of small samples of marked and unmarked members which tend to have negative binomial distributions due to schooling.

Although the survival rates be assumed constant during all the time intervals, the sampling would have to be uniform over the sampling intervals, or perhaps more ideally the sampling should be concentrated at the midpoint of each sampling interval. With small, highly mobile, and schooling populations as the Ikroavik Lake whitefishes, sampling adequate numbers at will was impossible with the available gear. Actually the first *Coregonus nasus* were taken on July 15 and the first *Leucichthys sardinella* were taken on July 30. The last day on which either species was taken was on September 10. As far as the *L. sardinella* data of Table I are concerned, the bulk of the fish were sampled near the middle of interval $t = 0$, at the beginning and end of interval $t = 1$, and near the middle of interval $t = 2$. The *C. nasus* data of Table II are from sampling concentrations in the middle of interval $t = 0$, rather near the beginning of interval $t = 1$, and slightly before the middle of interval $t = 2$. Thus, on the basis of sampling effort alone, the estimated three-week survival rate for *L. sardinella* may be considered relatively unbiased; on the same basis, the four-week survival rate for *C. nasus* would be somewhat biased.

Another source of bias may be the occurrence of a variable rate of survival for fish of different ages. The deterministic models used in this study would yield an "average" survival rate. If age-specific mortality existed, survival rates could be computed from capture-recapture data pertaining to individual age groups; in this instance each fish would have to be aged and the sampling would ordinarily have to be prohibitively intensive if there were many age groups which had to be evaluated individually.

Although the capture-recapture data for both species are quite limited and the estimated survival rates have large standard errors, there is evidence on other grounds that the survival rate estimates for *Leucichthys sardinella* are of a reasonable magnitude. Although there was a small amount of mortality introduced by the removal of 50 *L. sardinella* and 3 *Coregonus nasus*, these removals would introduce a very small error. However, in the case of *L. sardinella* taken by seine, perhaps one per cent of the specimens, which were otherwise undamaged, had very little vigor and were seemingly near death. (These particular moribund individuals were not marked and released but were included among those removed.) The simple indication is that the fraction (*ca.* 0.01) of moribund *L. sardinella* among vigorous specimens appeared to be of the same order as the estimated summer rates (0.007 to 0.012). Therefore it may be concluded that the capture-recapture technique of estimating mortality rates was generally successful. The value of these methods is especially enhanced because the same data can be used for estimation of population size by the Schnabel (1938) or similar methods as used by Wohlschlag (1953).

On the assumptions of no differences in year to year (time-specific) mortality rates, constant recruitment to the various age classes in past years, and random sampling of age groups five to eleven, the *L. sardinella* catch-curve data (Table III and Figure 1) suggest a survivorship curve resulting from age-specific mortality rates which increase with age. (See Ricker (1948) for a detailed discussion of catch-curve interpretation.) Deevey (1947) has pointed out the difficulties of evaluating catch-curve data for the derivation of suitable survival and mortality rates. Such difficulties arise from gear selectivity whereby the older fish

are not taken in proportion to their true abundance, from irregularities in year to year recruitment, and from selective removal of certain age groups by a fishery. The first difficulty apparently was not of serious proportions for the *L. sardinella* sampling. A special effort to capture the larger *L. sardinella* was made by use of a 2½-inch bar mesh gill net during the July-August seining operations; no fish were taken. Only two *L. sardinela,* aged 11 and 8 years, were retained by the 2-inch meshes of the experimental gill nets during the September samplings; these two fish were exceeded in size by about 30 fish taken in gear with smaller meshes. Furthermore the seine and gill-net samples were essentially similar on a size-frequency basis, and except by chance it would seem unlikely that two such diverse types of gear should have the same biases in retaining the older fish. The regularity of the catch-curve above age five as plotted in Figure 1 indicates that recruitment must have been fairly regular in past years. It should be recognized that a curve of the shape indicated could be due to continuously decreasing recruitment, or to mortality increasing with age (age-specific mortality), or to mortality decreasing with time (time-specific mortality), or to chance fluctuations. It is difficult to conceive how either a long term trend of decreasing recruitment or decreasing time-specific mortality could have been brought about in the essentially isolated population of Ikroavik Lake. However, if the older fish do die at greater rates in Ikroavik Lake there is no readily apparent reason. The lake has no fishery and no piscivorous fish, and predation by birds such as loons would be directed toward the younger fish. Any age-selective effects of parasitism were not obvious, since only about five per cent of all sizes of *L. sardinella* were noticeably parasitized. The only clear difference between fish or five to eight and eight to eleven years old is that the older group included all sexually mature fish which could have conceivably experienced higher mortality rates in connection with spawning. If no age-specific mortality be admitted and if the size of the year classes has varied at random, the slope of the "best" straight line through the right limb of the catch-curve (Fig. 1) would yield an unbiased estimate of the mortality rate. As far as can be ascertained, there never has been appreciable exploitation of this species in Ikroavik Lake, and there has been virtually no fishing in the lake since 1944. Even if there had been a fishery, small species like *L. sardinella* would have been scarcely exploited by the large meshes of the gill nets customarily used by the Eskimo.

When the *L. sardinella* mortality rates are reduced to average daily expectations of death, comparison of the summertime rates with the estimates derived from yearly rates becomes possible. The daily summertime expectation of death, estimated from 0.007 to 0.012, is from data pertaining to all size groups above 180 millimeters and age-class five. Compared to even the highest daily age-specific rate of 0.0038 for fish between ages eight to ten (Table III), the summer rate is about twice as great; and the summer rate is still greater than the other age-specific rates or the average daily rate of 0.0027 calculated on the basis of no age-specific mortality (Fig. 1, broken line). These comparisons mean that the summertime mortality rate must be higher than the average over the entire year, if the daily rate of 0.007 to 0.012 for the summer is anywhere close to the correct magnitude. The conclusion that the summer mortality is greater than winter mortality is especially interesting, since the resident population in winter and spring is confined under six feet of ice cover in no more than 18 inches of water. That death rates vary with the water temperature is at least suggested by the fact that fish taken during September when the water temperatures were near freezing did not have to be handled so carefully to prevent deaths as they did when the water temperatures rose briefly above 10 degrees Centigrade in mid-August.

From the growth data compiled by Cohen (1953) for *Leucichthys sardinella,* all indications point to the fact that the peak of growth coincides in a general way with the summer peak of natural mortality in Ikroavik Lake. The way in which mortality and growth peaks are distributed with time are, of course, extremely important in defining the nature of population dynamics with respect to the magniture of biological production and appropriate times during the year when exploitation can be carried out with the greatest yields per unit of fishing effort.

There appears to be no evidence that *Coregonus nasus* are ordinarily numerically dominant over the other species in arctic and subarctic lakes. This condition was true in Ikroavik Lake, and according to the Barrow Eskimo, it was also true of other lakes in the Point Barrow region. Of the 73 *C. nasus* aged by Cohen (1953), the youngest were three years old, and 21 were 10 to 15 years old. Allowing for irregular recruitment, this information would tend to suggest that the older fish had reasonably low mortality rates, so that the explanation of the small Ikroavik Lake population of several hundred fish can be made only when additional data on fecundity and mor-

tality rates from egg stages through the first several years of growth become available.

Summary

In unexploited Ikroavik Lake near Point Barrow, Alaska, summertime mortality rates of *Leucichthys sardinella* and *Coregonus nasus* were determined by mark-and-recapture methods described by Leslie and Chitty (1951) and Bailey (1951). The application of these techniques is discussed in detail and it is concluded that they are feasible if sampling can be carried out on a sufficiently large scale, particularly in conjunction with other studies involving mark-and-recapture operations.

Catch-curve data suggest that the older *L. sardinella* die at greater rates than do middle-aged fish. All available evidence indicates that the *L. sardinella* die at greater rates during the summer than during the remainder of the year when the population is confined to very little water under a thick ice cover.

No explanation of the reason why the *C. nasus* population is so small appears to be evident from the limited mortality data available.

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THE INFLUENCE OF SHADE AND LITTER OF PINE ON EVAPORATION FROM A CLAY LOAM SOIL AT BERKELEY, CALIFORNIA

JOSEPH KITTREDGE[1]
School of Forestry, University of California, Berkeley, California

Evaporation from the soil is one of the ways in which water from precipitation is lost for human use. Part of the loss is water in excess of the field capacity of the soil which might replenish streams and part is capillary water which must be replaced by rainfall that might otherwise be available for streamflow. In other words, both detention storage and retention storage are reduced by evaporation. In a region of long dry summers when lack of water may become critical, it is important to know the magnitude of the losses of water by evaporation and how they may be reduced. The purpose of this investigation was to determine the losses by evaporation from a bare soil and by comparing them with the losses from the same soil under the shade and litter of a dense stand of pine, to determine the influence of the forest on the evaporation.

LOCATION AND METHODS

The plots were located about ½ mile east of the University of California campus at an elevation of 800 feet on a south-facing slope of 40 per cent. The annual rainfall of 24 inches more or less, falls mostly in the months from December through March. Fogs occur often in the summer months but fog drip under the pines rarely amounted to 0.01 inch. The soil is classified as a Los Osos clay loam and is underlain by soft sandstone at depths of 3 or 4 feet. The natural grassland had been heavily grazed for many years before the cattle were excluded by a fence in 1932. The Canary Island pine (*Pinus canariensis* C. Smith) was planted in 1912 and had formed a stand 45 feet high with crown coverage of 85 per cent and no undergrowth. The forest floor covered 100 per cent of the area, had a depth of 3 inches, volume-weight of 0.04 and amounted to 12.6 metric tons per acre in 1940.

The soil was sampled at 1 to 7 day periods after each rain in 2 inch layers down to 14 inches and in 1941 down to 20 inches in two small plots, that were trenched periodically to cut off all roots of surrounding vegetation with the intent of eliminating loss of moisture by transpiration. After the roots were cut, the trenches were refilled with soil. One plot in the grassland was kept bare of vegetation and the other, about 100 feet to the west at the same elevation, was assumed to differ only by the covering of forest floor and shade of the crowns of the pines. The close similarity of the mineral soils of the two plots is indicated by the figures for moisture equivalent all between 26.5 and 30.1 per cent including differences between forest and open and at different depths. The forested soil had slightly more organic matter, from 8.13 per cent in the upper 2 inches to 5.81 per cent in the 6-8 inch layer, than the denuded with corresponding percentages of 8.04 and 5.22. Most of the samples were taken with a 2-inch length of pipe, 1⅝ inch inside diameter, and bevelled to a cutting edge at one end. The samples were dried for 24 hours in an oven at 105°C and the dry weights were used in the computation of volume-weights and depths of water above the oven-dry content. The depth of water (d) derived as the product of percentage soil moisture (M/100), volume-weight (σa) and depth of soil (D), that is, $d = \frac{M}{100} \times \rho a \times D$, represents the depth of liquid water that would result if all the water above the oven-dry condition were extracted from the soil and measured for depth in a container of the same diameter as that of the soil sample. Differences in depth of water on successive dates of sampling in periods without rain were used as measures of evaporation although frequent gains in moisture during rainless periods obviously indicated that the figures actually represented the combined results of evaporation, condensation, and other less evident processes.

Volume-weights varied between 0.9 and 1.5 in samples on successive days and only a few inches apart. Six-inch samples taken with a King tube were compared with the sums of three 2-inch samples on the same dates. The King tube samples were more variable and tended to be lower particularly when the soil was wet. Determinations on a number of clod samples by the paraffin immersion method gave volume-weights about 0.2 higher than those by the other methods, doubtless because the clods had smaller propor-

[1] The author gratefully acknowledges the effective help of the following graduate student assistants who took part in the field or office work as it progressed: H. W. Anderson, H. L. Baker, H. W. Fiedler, R. F. Grah, E. J. Hodgkins, A. P. Mazurak, E. L. Schmahl, C. C. Wilson, and L. B. Zulick.

tions of macropores than did the soil as a whole. The volume-weights finally used in computing depths of water were the medians of 85 to 185 determinations for each 2-inch layer by the 2-inch pipes after the obviously erroneous values obtained from very wet or very dry soil had been rejected. The medians in the open varied from 1.11 to 1.21 and under the pines, from 1.16 to 1.32. The highest values were found below 12 inches.

The combined effect of meteorological factors other than rain was indicated by the measurements of evaporation from a free water surface in standard Weather Bureau pans, one under the pines and the other in the grassland. Rainfall, interception and stemflow in this area have been reported previously (Anderson and Kittredge 1953, Hayes and Kittredge 1949 and Kittredge, Loughead, and Mazurak 1941).

The analysis includes not only the depths of water evaporated from the soil and the differences in depth between forested and exposed bare soil as indicating the influence of the shade and litter but also the changes in evaporation associated with changes in depth below the surface, in moisture content, in time since rain, and in evaporation from a free water surface.

Previous Work

Recent studies of evaporation from bare soil like the earlier ones, illustrate the many factors that are involved and the consequent variation and uncertainty of generalizations. By combining the vapor pressure difference and energy balance functions, Penman (1948) has derived a formula by which evaporation from open water can be estimated from air temperature, dewpoint temperature, wind velocity, and daily duration of sunshine. For bare wet soil in England the evaporation was 0.9 and with the water table at 5 inches below the surface, it was from 0.8 to 0.54 of that from a water surface. Earlier he suggested that evaporation from fallow soil (E) was related to number of days of exposure (T) by the equation, $E = aT^b$, where a had values of 0.5 or 0.6 and b, from $\frac{1}{3}$ to $\frac{1}{4}$ (Penman 1941). At North Fork, California, Anderson (1946) found that evaporation rate in percentage of soil moisture per day (E%) could be represented as $E\% = -176.7\ t^{-1}\ N^{-1.2}$ where t is mean air temperature in degrees F. for the 21 days prior to the moisture determination and N is number of days since rain. From lysimeters 21 inches deep also at North Fork, Rowe (1948) reported mean annual evaporation at the daily rate of 0.03 inch from bare soil and 0.02 inch from soil covered with 2 inches of ponderosa pine litter. In the same area during the summer drying period, Rowe and Colman (1951) found an average rate of loss from the upper three feet of bare soil of 0.06 inch per day. From 6 feet of soil at Bass Lake, the rate was 0.07 and from 5 feet of soil at the San Dimas Experimental Forest, it was 0.075 inch per day. In experiments with sand, Woodruff (1941) determined ratios of soil to water evaporation that decreased from 1.0 to 0.03 as the sand dried. After the surface was dry, the evaporation was proportional to the depth of the dry layer. From a silt loam soil in Nebraska, shading reduced evaporation to 64 per cent and 1½ inches of straw mulch to 27 per cent of that from the exposed bare surface (Russel 1939). A stand of Jeffrey pine in the San Bernardino Mountains according to Munns,[2] reduced evaporation from soil boxes 1 foot deep to 66 per cent of that in the open.

Gains of soil moisture often alternate with losses and reduce the net evaporation. Condensation on the large grass-covered lysimeters at Coshocton, Ohio, varied seasonally from about 0.03 inch per day in the winter to 0.01 inch in the summer months (Harrold and Dreibelbis 1951). In Indiana, condensation on bare soil occurred 300 nights a year and averaged 0.002 inch in depth with a maximum of 0.01 inch per day (Cotnoir and Kohnke 1947). More recently in the same area, gains by adsorption and condensation of atmospheric water vapor have been estimated at 1.22 inches per year with an additional 1.34 inches by water vapor transfer from the subsoil, making a total annual gain of 2.56 inches (Brawand and Kohnke 1952). Still another estimate of upward movement of water vapor was 1.72 inches from October to March (Jones and Kohnke 1952). In experiments at Davis, California, when evaporation was prevented, the movement of water vapor was upward from September to January at a maximum rate of 0.001 inch per day and downward from January to August at a maximum rate of 0.02 inch per day (Edlefsen and Bodman 1941). In closed columns of soil, Gurr, Marshall, and Hutton (1952) found a transfer of water from the hotter toward the colder end and the maximum net transfer in soils with initial moisture content equal to ⅓ the moisture equivalent. Movement in the liquid phase occurred at pF of 3.9. They suggest a continuous circulation in response to a temperature gradient in which water evaporates from the hotter soil, moves as vapor into the colder soil where it condenses and returns as a liquid. The accumulation of liquid water under highway surfaces is ascribed to temperature changes by Winterkorn (1944). The film water

[2] From the manuscript, "Studies of forest influences in California" by E. N. Munns in the files of the U. S. Forest Service.

absorbed and strongly held on the soil particles at lower temperatures becomes free water at higher temperatures when the surface tension decreases because gravity causes the water films to thicken on the lower sides of the particles and finally drops form which drip off as free water. When the temperature falls again, this water is not available to replenish surface films above and more water vapor is captured from the air. These various findings lead to the expectation that evaporation from year to year, from season to season and from day to day will be widely variable.

Forest Influence on Total and Seasonal Evaporation

The effect of the littter and shade of the pines in a single figure based on data of periods without rain for all four years was to reduce the evaporation from the upper 12 inches of mineral soil to 87 per cent of that from the bare unshaded soil. The corresponding percentage for evaporation from the free water surfaces in the pans was 41, a surprisingly large difference. Evidently the differences in meteorological factors above the soil constituted not more than half the cause of the difference in evaporation from the soil. These overall averages when subdivided by seasons give the following comparisons.

	Evaporation in forest as per cent of open	
Season	*Soil*	*Free-water surface*
December-February	153	48
March-May	72	37
June-August	60	30
September-November	118	49
Year	87	41

In each season, the ratio of evaporation under forest to that in the open for the water surface was one-half or less than one-half of that for the upper foot of soil, a comparison quite inconsistent with the fact that the soil was both shaded and litter covered whereas the water was only shaded. Moreover, the effects of the forest for both water and soil were greater in spring and summer than in fall and winter. In fact, fall and winter evaporation from the soil under the pines was greater than that in the open by 18 and 53 per cent respectively. In spring and summer on the other hand, evaporation from the soil under the forest was about two-thirds of that in the open. The difference between the two halves of the year was much greater from soil than from water.

While these percentage relatives suggest some relations as would be expected between evaporation from soil and from water, the graphs of daily depths of evaporation from soil plotted over those from water showed no trends of increase or decrease either in the forest or in the open. In other words, rate of evaporation from the soil did not change in any systematic way with a change in rate of evaporation from a free water surface and consequently, evaporation from a water surface did not provide an index of evaporation from soil.

The relation between daily evaporation from the upper foot of soil under the pines (Ef) and that in the open (Eo) tended to show a linear increase such that a change of 0.03 inch in the forest was associated with a change of 0.1 inch in the open ($Ef = 0.3\ Eo + 0.015$). However, there was wide dispersion and the regression would not be reliable as a basis for estimation of individual amounts and perhaps not for means. The daily rates of evaporation from the upper 2 inches showed no correlation between forest and open. The graph of cumulated evaporation showed an ill-defined slow increase until the evaporation in the open reached 0.3 or 0.4 inch and thereafter a rapid and accelerating increase. The trends for different years were not the same and again the relation is not a usable one. This accelerating trend is doubtless a result of the greater amount of soil moisture that remained under the pines after the soil in the open had become so dry that evaporation was reduced in comparison with that from the moister soil under the shade and litter.

Forest Influence on Cumulative Evaporation

During a rainless period following a rain, as the soil becomes drier, partly as a result of evaporation, the rate of evaporation tends to become smaller because less moisture remains to evaporate. However, the daily rates for short periods were highly variable doubtless because of differences in atmospheric humidity, in amount of cloudiness and fog, in wind movement, and in vapor pressure gradients within the soil and between soil and air. The variation extended widely not only within the range of evaporation but also beyond it to include frequent gains of moisture from the atmosphere or from deeper layers of the soil in excess of evaporation during the same period. Consequently the wide dispersion of the points when plotted did not provide satisfactory definition of trends. Cumulative evaporation when plotted over time-since-rain reduced the dispersion and was used in the analysis. All of the trends rose steeply for the first few days and then gradually became flatter with increasing time and dryness of the soil.

After the first 2 to 6 (and in one period, 13)

days, the trends were essentially linear on log-log paper and could be expressed in the form log $E = b \log T + \log a$ or $E = aT^b$, where E is evaporation in inches of water and T is time in days. In the open, the range in the slopes (b) of the logarithmic trends is from 0.24 to 0.62. The slopes under the shade and litter are less steep than in the open except in the one winter period. They vary from 0.15 to 0.67, and with exceptions, decrease as do those in the open. The "a" values are all between 0.55 and 0.08 and show a slight tendency to increase as the "b" values decrease. The differences in "a" between forest and open are small and not consistent.

The rate of evaporation per day may be computed by differentiating the equation, $E = aT^b$ to give $dE/dT = abT^{b-1}$ and substituting any desired values of a, b and T. For example, if a and $b = \frac{1}{3}$ and $T = 8$ days the rate of evaporation would be 0.028 inch per day and at $T = 80$ days, it would be 0.006 inch per day.

Other data were analyzed to try to discover factors that might be associated causally or otherwise with the differences in evaporation from the soil. The rates of evaporation from free water surfaces of 0.07 to 0.23 inch per day in the open as compared with 0.04 to 0.06 in the forest, although they are in the same direction, suggest much larger differences in evaporation from the soils than were found. Moreover, the sequence of values of evaporation from water for the different periods is not the same as that from soil. Thus, the climatic differences between forest and open only partially account for the differences in evaporation from the soil.

The periods in different seasons of the year as well as in different years might be characterized by differences in climate and soil moisture that should be reflected in evaporation from the soil. Actually, the one winter period had high values of b and low values of a, not very different from those for the three summer periods from May to September or October. The four spring periods in April and early May formed a group with low values of b and high values of a. This seasonal difference between spring and summer might be more significant if the periods did not all start after rains that wetted the soil. These three seasonal groups are more nearly distinct than are the trends for individual periods within the groups.

After a rain when the soil is wet, evaporation is more rapid than it is later as the soil dries. The logarithmic trends represent these later periods starting 2 to 6 days after rain (12 and 13 in one period). This corresponds to the 2 to 5 days usually considered as the time for a soil to dry to field capacity after a rain. In several periods, the soil in the forest was at or a little above the moisture equivalent, assumed to represent field capacity, at the start of the period of logarithmic trend. More frequently it was below and in the summer of 1939 the percentages of moisture were only 16 and 17. This was the period in which 13 and 12 days elapsed before the trends became linear. However, the constants of the trends for this period do not noticeably reflect the influence of the dry soil. Apparently the small differences in initial moisture content of the soil were not important in determining the trends of evaporation with time.

For depths of soil other than 12 inches, the trends would be different. Values of the constants for the upper six inches of soil indicated by comparison that as the soil layer was more shallow, the b values for slope increased while the a values decreased, or more simply, the evaporation changed more rapidly. Thus, the upper two inches should be more sensitive than the deeper layers in reflecting changes in evaporation.

An expression for cumulative evaporation that would cover the whole period after rain obviously would be more useful than the foregoing logarithmic relations that do not include the first few days of rapid evaporation. For this purpose, the equation applicable to other processes of exhaustion fitted the data reasonably well. It is, $E = M(1-e^{-KT})$, where E is depth of evaporation in inches, M is the maximum evaporation in inches that would occur if the time (T) were sufficiently prolonged and which the trend approaches asymtotically, e is the base of natural logarithms, 2.718, T is number of days since rain, and K is an empirical constant governing the rate of increase of the trend. Both M and K are constants for a given set of conditions but may be expected to differ for different periods or seasons or years and for different layers of the soil. Values of K and M for the upper foot of bare soil and of soil under shade and litter are arranged in descending order of K for bare soil in Table I. The values of K were derived by a process of trial and error as those which gave the best fits to the plotted trends as judged by eye and are therefore only approximate, although it is believed the value determined by the method of least squares would differ by less than 0.01 for any period. For the bare soil, the range in the values of K is from 0.02 to 0.12, and under the pines it is about the same, from 0.013 to 0.15. For single periods, the differences between forest and open are small. Some are positive and some are negative. Apparently, therefore, if the value of K reflects the influence of the shade and litter on evaporation, that influ-

TABLE I. *Evaporation in inches (E) from the upper 12 inches of bare soil in the open and of litter-covered soil in the shade of the pines in relation to number of days since rain (T) expressed as* $E = M\ (1-e^{-KT})$

Group	K Open	K Forest	M Open inches	M Forest inches	Moisture content				Computed evaporation in 10 days		Period
					Initial		Final				
					Open per cent	Forest per cent	Open per cent	Forest per cent	Open inches	Forest inches	
I	0.02	0.013	2.5	1.6	29	31	11	21	0.45	0.19	May 13-Oct. 17, 1941
	.02	.03	1.3	2.2	14	26	10	20	.23	.57	July 19-Aug. 30, 1940
	.025	.04	1.6	2.4	26	30	15	13	.35	.79	May 9-Sept. 20, 1938
	.03	.045	1.0	0.9	17	17	12	13	.26	.32	May 26-Aug. 29, 1939
II	.03	.08	1.6	1.4	25	20	22	16	.42	.77	Jan. 7-21, & Feb. 13-26, 1939
III	.04	.05	2.1	2.0	29	29	24	29	.69	.78	April 5-24, 1940
	.09	.08	1.1	0.9	25	16	18	14	.65	.50	April 5-May 5, 1939
	.12	.08	1.1	0.6	30	30	24	28	.77	.33	April 26-May 14, 1940
	.12	.15	1.1	0.8	29	31	23	29	.77	.62	April 15-28, 1941

ence is not consistent in different periods and years. Between seasons however, there are differences. In summer, K is less than 0.05 and in spring, it is more than 0.04. The values for winter are intermediate.

The depth of soil water subject to evaporation, represented by M, varies from 1.0 to 2.5 inches in the open and from 0.6 to 2.4 inches under the pines. The values of M are lower in the forest than in the open except for two of the summer periods. They tend to be lower in spring than in summer which may be an effect of the length of period rather than of season. The initial and final percentages of soil moisture, also given in Table I, are not sufficiently correlated with the values of K and M to be useful in accounting for the variation.

The evaporation in 10 days computed by the use of the equation, given in Table I, ranges from 0.23 to 0.77 inch in the open and from 0.19 to 0.79 in the forest. The average daily rate of evaporation for the first 10 days after rain may be obtained by dividing the figures by 10. Similar computations may be made for other periods of time quite easily by the use of a table of exponential functions that gives values of e^{-x} for different values of x. The maximum difference between forest and open was 0.44 inch, the amount by which the open was in excess in April and May, 1940 and also, the amount by which the forest was in excess in the summer of 1938. The excesses and deficits in other periods are about equally divided so that a generalization as to the influence of the forest on evaporation from the upper foot of soil is not justified. Depths of ten-day evaporation computed by the use of the formula, $E = aT^b$, are not very different from those in Table II and the relations between forest and open are nearly the same.

VARIATION OF EVAPORATION WITH DEPTH IN SOIL

An approach to the evaporation at different depths in the soil was made by plotting cumulative evaporation for each 2-inch layer and fitting the curve, $E = M\ (1 - e^{-KT})$, so that the constants K and M could be used as measures of changes with depth and as a basis of comparisons between forest and open at different depths. Among the four periods used as examples including the two in Table II, there are exceptions to almost any general statement that might be made. The values of K for the upper 2-inch layer are .03 to .05 smaller in the forest than in the open but the difference is frequently reversed below 2 inches. In the forest below 4 inches, K is larger than in the open except in 1941 below 12 inches when 0.005 was lower than 0.01 in the open. In the open down to 6 inches, the values of K decrease with depth but at greater depths and at any depths in the forest, this trend may become an increase particularly below 10 inches. Except in the 0-2 inch layer the values of K rarely exceed 0.10.

Values of M decrease with depth with minor exceptions. They may be either smaller or larger

TABLE II. *Evaporation in inches (E) from 2-inch layers of bare soil in the open and of litter-covered soil in the shade of the pine in relation to number of days since rain(T) expressed as* $E = M\ (1-e^{-KT})$

April 5-May 5, 1939

Soil depth inches	K Open	K Forest	M Open inches	M Forest inches	Initial moisture content		Computed evaporation in 30 days		Average daily evaporation			
									0-5 days		10-30 days	
					Open per cent	Forest per cent	Open inches	Forest inches	Open inches	Forest inches	Open inches	Forest inches
0-2	0.17	0.12	0.42	0.17	25	19	0.41	0.17	0.048	0.008	0.004	0.002
2-4	.12	.07	.21	.16	27	19	.20	.14	.018	.006	.003	.003
4-6	.05	.07	.12	.16	24	19	.10	.14	.005	.006	.003	.003
6-8	.05	.12	.12	.16	25	20	.10	.16	.005	.009	.003	.002
8-10	.05	.15	.12	.14	26	20	.10	.13	.005	.007	.002	.001
10-12	.07	.10	.12	.16	26	21	.11	.15	.007	.008	.002	.002
12-14	.07	.10	.12	.19	27	23	.11	.18	.007	.010	.002	.003
					May 13-October 17, 1941							
0-2	0.05	0.01	0.55	0.46	29	36	0.43	0.12	0.024	0.004	0.011	0.004
2-4	.015	.01	.52	.34	30	33	.19	.09	.007	.003	.006	.003
4-6	.01	.015	.48	.25	31	31	.12	.09	.005	.004	.004	.003
6-8	.01	.015	.38	.24	29	30	.10	.09	.004	.003	.003	.003
8-10	.01	.01	.33	.20	28	28	.09	.05	.003	.002	.003	.002
10-12	.01	.01	.33	.24	29	28	.09	.05	.003	.002	.003	.001
12-14	.01	.005	.28	.22	27	27	.08	.03	.003	.001	.003	.001
14-16	.01	.005	.30	.18	28	26	.08	.03	.003	.001	.002	.001
16-18	.01	.005	.31	.16	29	25	.08	.02	.003	.001	.003	.001
18-20	.01	.005	.32	.14	29	24	.08	.02	.003	.001	.002	.001
0-20	...	...	...	...	..	..	1.34	.59	.058	.022		

in the forest than in the open even when the initial moisture contents under the two conditions are the same. Higher values of M tend to be associated with higher percentages of moisture.

Perhaps clarification is needed for a statement that evaporation from the 2-4 inch layer is smaller than that from the 0-2 inch. Quite simply it means that moisture moves less rapidly from the 2-4 inch to the 0-2 inch layer than it leaves the 0-2 inch layer by evaporation into the atmosphere.

The evaporation in 30 days computed from the equation varied from as much as 0.43 inch from the upper 2-inch layer of a moist soil in the open to as little as 0.02 inch from the 16-18 and 18-20 inch layers under the forest. The depth of evaporation generally decreased with depth below the surface and mostly rapidly in the upper 4 inches of soil in the open. The exception in May, 1939 in the open was evidently a result of the dry soil with only 8 per cent moisture in the upper 2 inches compared with 15 per cent in the 2-4 inch layer. That summer of 1939 had the driest soil and also the lowest evaporation down to a depth of 6 inches. For the other three periods, the decreasing trend of evaporation (E) with depth (D) in the open down to 10 inches can be represented approximately as $E = 0.4D^{-.78}$. For the forest data, the trends are not linear on log-log paper but become linear on semi-log paper for the spring of 1939 and the summer of 1941 so that they can be expressed as log E = —0.05D-0.72 and log E = —0.045D-0.85. The two trends have nearly the same slope and could perhaps be combined. The trend for 1938 for the bare soil is also essentially linear on semi-log paper and thus provides a comparison with the forested soil. The equation is, log E= —0.14D-0.31, expressing the steeper rate of decrease with depth. These quantitative comparisons are derived from periods when the initial soil moisture was nearly the same at all depths and not far from field capacity. They would not be applicable when soil moisture varied with depth as in the summer of 1939 in the open. Below 10 inches and more noticeably in the open, evaporation increased slightly with depth although in 1941 the decreasing trend continued down to 20 inches depth. Evaporation under the shade and litter was lower in some periods and higher in others than that from bare soil in the open.

The average daily evaporation for the first five days after rain decreased with depth as did the 30-day evaporation. Only two rates were greater than 0.02 inch per day. Most of the rates were less than 0.01 inch. Below 8 inches the rates were as low as 0.001 inch per day in two seasons. Differences between forest and open were not consistent. The rates for the 10-30 days after rain were all lower than 0.012 inch per day and most

of them lower than 0.005 inch. Trends with depth were less steep and differences between forest and open were smaller than in the 0-5 days.

The distribution of evaporation with depth in 1941 when the sampling extended down to 20 inches and the percentages of moisture were quite uniform, indicates the large part of the total that is derived from the upper layers of the soil as shown in Table III. The percentages of the total evaporation from different layers decrease with depth, but there is no evidence of a definite depth of 12 inches more or less below which evaporation becomes negligible. Roughly 80 per cent of the evaporation came from the upper 12 inches. About one half the evaporation was from the upper 4 inches in the open and from the upper 6 inches in the forest. In the open, the proportion of the evaporation from the 0-2 inch layer is much larger than in the forest, but under the shade and litter, from the 2-12 inch depth, the reverse is true.

TABLE III. *Distribution of evaporation with depth in the soil for the period May 13-October 17, 1941*

Depth inches	30-day totals				Daily rates in the first five days			
	Open		Forest		Open		Forest	
	Per cent of total	Cumulative per cent	Per cent of total	Cumulative per cent	Per cent of total	Cumulative per cent	Per cent of total	Cumulative per cent
0-2	32	32	20	20	42	42	18	18
2-4	14	46	16	36	12	54	14	32
4-6	9	55	15	51	9	63	18	50
6-8	7	62	15	66	7	70	14	64
8-10	7	69	9	75	5	75	9	73
10-12	7	76	8	83	5	80	9	82
12-14	6	82	5	88	5	85	5	87
14-16	6	88	5	93	5	90	5	92
16-18	6	94	4	97	5	95	4	96
18-20	6	100	3	100	5	100	4	100
0-20	100=1.34 in.		100=0.59 in.		100=0.058 in.		100=0.022 in.	

Variation of Evaporation with Soil Moisture

The influence of moisture content of the soil on evaporation was explored by plotting daily depths of evaporation over percentage soil moisture for the 0-2, 2-4 and 4-6-inch layers where changes were most often large and prompt. Data for several years were combined to provide a wide range of moisture contents. The arrays for forest and open both indicated accelerating trends with wide dispersion of individual points including many for short periods when gains of moisture exceeded losses by evaporation. The trends were linear on log-log paper and thus daily evaporation in inches (E) was related to percentage moisture content (M) by the equation, $E = aM^b$. Values of a and b and of computed evaporation for forest and open for the three layers are given in Table IV. The equations for bare soil applied to moisture contents between 15 and 30 per cent while those for the forest, between 17 and 35 per cent. The relation between daily evaporation and soil moisture takes the same form at different depths but the two constants a and b change with depth. The values of "a" decreased with depth while those for the exponent "b" increased. More specifically, evaporation increased in the upper two inches approximately as the 2.5 power of the percentage of soil moisture, in the 2-4 inch layer, as the 4.3 to 5.8 power and in the 4-6 inch layer, as the 6.6 to 7.1 power. The computed values of evaporation decrease as soil moisture decreases both from bare soil and from the soil under litter and shade. The evaporation in the forest is ¼ that in the open at all three moisture contents in the 0-2 inch layer. In the 4-6 inch layer, it is twice that in the open. In the 2-4 inch layer, at 30 per cent moisture, the ratio of forest to open is 0.6, at 25 per cent, 0.4 and at 20 per cent, 0.3. The foregoing analysis may have some value in suggesting the form of the relations and the order of magnitude of the constants, but it is doubtful whether the equations should be used to estimate evaporation from soil moisture and certainly the constants should not be used without checking for other conditions of forest and soil.

Most of the relations that have been explored have seemed of questionable usefulness because of the wide dispersion of the data about trend lines, and in general, variation that was not explained by the variables measured. One of the disconcerting phenomena was the frequent occurrence of gains in soil moisture during short periods without rain, in amounts larger than would be expected to result from condensation or movement of moisture from deeper layers of the soil. One specific and extreme example may be illustrated by the data of soil moisture for the period from 3 P.M. June 16 to 3 P.M. June 18, 1941. No rain had fallen since a shower of 0.09 inch on May 26 and 0.81 inch on May 13. For those three days, maximum temperatures were 68, 70, and 73 degrees F. and clouds or high fog occurred both morning and afternoon of the 16th and on the morning of the 18th. Evaporation from the Weather Bureau pan in the open was 0.29 inch, a little below average, and under the shade it was 0.09 inch, also a little below average for the month. Thus the climatic conditions apparently were favorable for evaporation even under the pines. The percentages of soil moisture in the open decreased slightly indicating total evaporation of 0.21 inch of water from the upper 12 inches of soil during

TABLE IV. *Depth of daily evaporation in inches (E) in relation to percentage of soil moisture (M) for 0-2, 2-4, and, 4-6 inch depths in soil of forest and open according to the regression,* $E = aM^b$

Depth inches	a		b		Computed evaporation					
					M=30		M=25		M=20	
	Open	Forest	Open	Forest	Open inches	Forest inches	Open inches	Forest inches	Open inches	Forest inches
0-2	1.3×10^{-5}	4.2×10^{-6}	2.58	2.50	0.084	0.021	0.052	0.013	0.030	0.0075
2-4	1.7×10^{-8}	6.1×10^{-11}	4.28	5.79	.036	.022	.017	.007	.0065	.002
4-6	6.0×10^{-13}	5.5×10^{-12}	7.08	6.63	.017	.033	.005	.010	.001	.002

the two days. All of which would lead to the expectation that there would be at least a little evaporation from the soil under shade and litter.

Actually however, the moisture content under the pines increased in all but the 14-16 inch layer. The increase amounted to 16.4 per cent in the upper 2 inches, 7.4 per cent in the 2-4 inch layer, and from 1.5 to 4.6 per cent down to 14 inches. From 14 to 20 inches, the changes were small although two of them were increases. The upper 12 inches of soil gained 0.92 inch of water in the two days of which 0.6 inch accumulated in the upper 4 inches of soil. How can such surprising increases be explained? All computations were checked and unlikely errors in weighing would rarely affect more than one figure in such a series where the sequence seems consistent. The small increases below 16 inches gave no evidence of upward movement of moisture from deeper layers such as occurred in some periods and of which an example has been reported previously (Kittredge 1949). However, the records from well-points installed in 1944 indicated that the water table even in storms of 1 inch or more that produced surface runoff, receded to at least 20 inches below the surface of the soil within 5 hours after the rain stopped and, with one exception, showed no rise within 30 inches of the surface under the pines in storms when rises were recorded in the grassland. Thus, the possibility of ground water as a source of the increased moisture must be discarded. The vapor pressure gradient in the soil under the shade and litter would be low and would not favor movement in the vapor phase. Moreover, the addition of water vapor, if any, would not increase the moisture content above field capacity to the 34.9 per cent in the 0-2 inch layer. The increases being largest near the surface and decreasing downward indicate that the moisture came from above. Vapor pressure gradients from air to soil would not be sufficient to cause transfer of more than small amounts of moisture. Condensation under the crowns and litter where cooling by out-going night radiation would be slight, would not deposit appreciable amounts of moisture. Fog is a possible source. The morning of June 18 was reported "cloudy" at an elevation 500 feet lower in Berkeley. This was doubtless high fog and it may have been one of the occasional nights when the fog was close to the ground at the 800 foot elevation of the experimental area. Records of fog drip from the crowns in this area have rarely shown as much as 0.01 inch. However, elsewhere amounts of 0.1 inch per day have been reported (Kittredge 1948). Lacking actual evidence, one may speculate that the surface layer of the loose needle-litter might intercept droplets of water from fog moving close to the surface and this water might run down through the litter into the mineral soil. Presumably this contribution of water would be smaller than that from fog drip because the vertical exposure of needles of litter would be much smaller than that of the crowns. No one or combination of these processes seems to account satisfactorily for the large increases of soil moisture. The frequent occurrence of periods when gains of moisture were recorded was an important source of variation that tended to obscure the definition of trends and relations.

The quantitative application of these findings to other areas of different soil and cover should be made only after checking. Moreover, because transpiration was eliminated in the plots, the moisture content and distribution of moisture were not the same as they would have been without the trenches and for the same reason the evaporation was higher than it would have been if transpiration had been going on concurrently.

SUMMARY AND CONCLUSIONS

A summary of conclusions may be made with the admission that some of them must be considered only as indications, and with the hope that indications may have some value.

1. Under the litter and shade of the pines, evaporation from the upper foot of soil from March through August was two-thirds and from September through February about five-fourths of that from bare soil in the open.

2. The corresponding fractions for a free water surface were about one-third and one-half. The influence of the forest on evaporation from soil was much less than from water.

3. An increase in daily evaporation from the upper foot of soil under the pines tended to be about 0.3 of the associated increase from the bare soil.

4. The trends of cumulative evaporation from soil with time as the soil dried, were steep for the first 2 to 6 days and thereafter increased more slowly at a decelerating rate which could be expressed as $E = aT^b$. The values of b ranged from 0.15 to 0.67 and for the same period, were lower in the forest than in the open. Differences in the values of a were not consistent.

5. Rates of evaporation from the upper foot of soil were from ½ to ¼ of those from free water surfaces.

6. Cumulative evaporation from the upper foot of soil for the whole period after a rain could be expressed approximately as $E = M(1-e^{-KT})$. Values of M were between 0.6 and 2.5 and were usually lower in the forest. Values of K were between 0.01 and 0.15 and did not reflect the influence of the forest consistently.

7. In the upper 2-inch layer of soil, values of K were smaller in the forest than in the open and below 4 inches, they were larger.

8. Values of M tended to decrease with depth.

9. Depth of evaporation decreased with depth below the surface most rapidly in the upper 4 inches of bare soil, and at a decreasing rate downward.

10. The rate of decrease with depth was more rapid in the open than in the forest.

11. Monthly evaporation from 2-inch layers varied from 0.43 inch from the upper 2 inches in the open to 0.02 inch below 16 inches under the pines.

12. About 80 per cent of the evaporation from the upper 20 inches of soil came from the upper 12 inches and 50 per cent from the upper four inches in the open and from the upper 6 inches under the forest.

13. Daily evaporation decreased as soil moisture decreased according to the equation $E = aM^b$ in which a and b varied with depth and also between forest and open.

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ECOLOGICAL STUDIES OF FOREST TREES AT CHALK RIVER, ONTARIO, CANADA

I. TREE SPECIES IN RELATION TO SOIL MOISTURE SITES[1, 2]

DONALD A. FRASER
Petawawa Forest Experiment Station, Chalk River, Ontario, Canada

INTRODUCTION

The important influence of natural conditions on tree growth is generally accepted but the literature discloses surprisingly few attempts at a critical detailed investigation. A study was therefore commenced in 1949 on environmental conditions and growth of various tree species in a limited forest plot. The studies were concerned with the physical ecology of hardwood stands and the growth responses of selected trees in healthy and decadent conditions. The work was centered at the Petawawa Forest Experiment Station, Chalk River (45° 58′ N. lat., 77° 31′ W. long.), because of special facilities available there including a well-established weather station and security against interference on any plot that might be established.

The present contribution is primarily descriptive of forest conditions in the experimental area. Future papers will be concerned with the physical ecology of the stand and seasonal growth of forest trees.

FOREST REGION AT CHALK RIVER

The forest at Chalk River constitutes part of Halliday's (1937) Great Lakes—St. Lawrence Region which extends from the Lake of the Woods district eastward to New Brunswick, the northern boundary being broken by Lake Superior. The area is bordered on the north by the boreal forest, and on the south of the deciduous forest. The climax-indicating species, according to Weaver and Clements (1938) are white pine (*Pinus strobus* L.) and hemlock (*Tsuga canadensis* (L.) Carr.), as well as some of the northern hardwoods including sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), yellow birch (*Betula lutea* Michx. f.), and beech (*Fagus grandifolia* Ehrh.). Less tolerant tree species include: aspen (*Populus tremuloides* Michx.), large-tooth aspen (*Populus grandidentata* Michx.), white birch (*Betula papyrifera* Marsh.) red pine (*Pinus resinosa* Ait.), and jack pine (*Pinus banksiana* Lamb.).

CLIMATE

The climate at Chalk River is continental-humid with extremes of heat and cold. The following data were derived from station records 1936-1950 inclusive (Anonymous 1952): the mean annual temperature is 39.4° F. and the lowest and highest temperatures on record are —38.2° F. and 98.1° F. The warmest month is July with a mean of 67.2° F. and the coldest, January with a mean of 8.8° F. The latest freezing temperature on record occurred on June 1 and the earliest on September 9, giving a minimum frost-free period of about 100 days, although this is unusual. The average growing season is 136 days. The average precipitation is 29.97 inches per year. Of this, the equivalent of 7.5 inches falls in the form of snow which covers the ground from November to April.

Climatic data alone have limited application in ecoclimatology. They are more useful for the study of growth and distribution of plants when they are combined into indices. Hare (1950) considers Thornthwaite's system (1948) as the best method of treating climatic data. In this system, annual potential evapotranspiration is the index used to establish the degree of thermal efficiency possessed by a climate. Hare places the Chalk River area in the thermal efficiency region with 20 inches of potential evapotranspiration and a moisture index of 80 which is classed as humid. The effectiveness of moisture conditions represented by these indices may be limited by edaphic conditions where run-off or seepage influences the availability of water to the plants.

SOIL SITES

Soil and its related variables, moisture and nutrients, present one of the most complex external factors in the study of forest ecology. It is proposed to establish a soil moisture—forest tree distribution relationship and to use the concepts developed therein to describe soil conditions in the experimental plot.

Ontario includes three major soil zones (Hills 1945), which correspond approximately to the

[1] Contribution Number 114, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.

[2] This is the first in a series of contributions on the ecology of forest trees at the Petawawa Forest Experiment Station, Chalk River, Ontario.

forest regions of Halliday (1937): the podzol zone in the north (boreal forest), the brown podzolic zone in the center (Great Lakes—St. Lawrence forest), and the gray-brown podzolic in the south (deciduous forest). The zonal profiles of these three soil zones show the following horizon modifications from north to south: The A_0 becomes thinner, the A_1 becomes thicker; the A_2 browner and less intensively leached, the B_2 thicker and the whole profile becomes deeper.

The horizons developed within the soil profile depend on many factors, including parent material, moisture regime, ecoclimate, vegetation, and time. Profiles from similar parent material and the same ecoclimate usually develop in proportion to their position in the soil moisture regime. Such a series of profiles is known as a "soil catena." Milne (1935) was the first to use the term "catena" to describe soil patterns related to drainage. Bushnell (1940) has applied the soil catena concept to the soils of Indiana, and Hills (1945, 1953) has used it in his decimal system of soil classification in Ontario.

For the present investigation, the development of the soil profile within the different moisture conditions has been arbitrarily divided into eleven units indicated by indices Θ (theta), 0 to 9 following the Milne-Bushnell-Hills system. Theta (Θ) indicates excessive drainage, whereas 9 represents a state of almost continuous saturation. The normal expression of both temperature and moisture, on which the climatic climax of Clements (1928) develops, occurs at index 2. This is known as the zonal profile. The range of profile developed may be illustrated thus:

Θ	0	1	2	3	4	5	6	7	8	9
Azonal	Intra-zonal		Zonal				Intrazonal			Azonal

At index Θ there is only slight differentiation of the soil horizons. At index 9 the soils are so wet that little or no leaching occurs. These soil moisture indices afford a valuable criterion in the study of tree growth—soil moisture relations. A similar range of indices has been established by Hills (1953) for soil pore pattern and ecoclimate. A three-digit expression (ecoclimate, moisture regime, pore pattern) is being used by various workers in Canada to evaluate site characteristics in reconnaissance studies (Anon. 1952, Fraser 1952).

The Experimental Plot

The eight-acre experimental plot (Fig. 1) was located in a stand of mature yellow birch, sugar maple, hemlock, and fourteen other tree species. It is ten surveyor's chains (1 chain = 66 feet) long, south to north, and eight chains wide. The soil is an old ground moraine of loamy sand mixed with stones and covers the bedrock to a depth of at least ten feet except for small areas in the northwest and southeast corners. In making the survey upon which the contour lines were established, a figure of 100 was arbitrarily chosen to represent the elevation of the southeast corner. Lines were drawn for each two-foot difference in elevation. A valley extends along the area approximately from south to north, entering along the center of the southern boundary, and leaving near the northeastern corner. During spring and early summer a small stream flows through this valley. The difference in elevation between this lowest part of the plot and the highest portions at the northwestern corner is 62 feet. Where slopes are steep there is slight sheet erosion.

The heavy lines on the map (Fig. 1) divide the area into soil moisture regimes envisaged by Milne (1935), and elaborated on by Bushnell (1942) and Hills (1945, 1953). It has been mentioned that, according to this system, the complete range of soil moisture conditions from extremely dry to almost continuously saturated is represented by eleven indices Θ (theta), 0 (zero) to 9. These soil moisture regimes are recognizable by their soil profiles except where this is interfered with by erosion. Soil moisture regimes 1 to 6 are represented on the map by large Arabic numerals. They were mapped according to characteristics of the soil profile as indicated by auger borings, soil pits, and other observations on the steeper slopes where erosion had interfered to some extent.

The plot was chosen partially because it included considerable variation in topography in a small area, but the complicated drainage pattern resulting from it, necessitated the grouping of the soil moisture indices, as for example on the area labelled 1-2 where it was not practical to divide the plot into a large number of smaller areas. The profiles corresponding to the indices on the plot are represented in Table I.

It will be noted that wetter conditions are reflected in a thickening of the organic layer (A_0) brought about by slower decomposition, and a less conspicuous leached layer (A_2), culminating in the extreme condition where the gley (G) horizon has risen high enough to modify both the A and B horizons. The gley layer, produced by the fluctuating water table, is very deep on the drier sites, rising with the water table until in moisture class 5-6 it has completely replaced the B horizon and become superimposed on the A_2.

The analysis of the various soil horizons removed from pit P1 located on moisture regime 3 is shown in Table II.

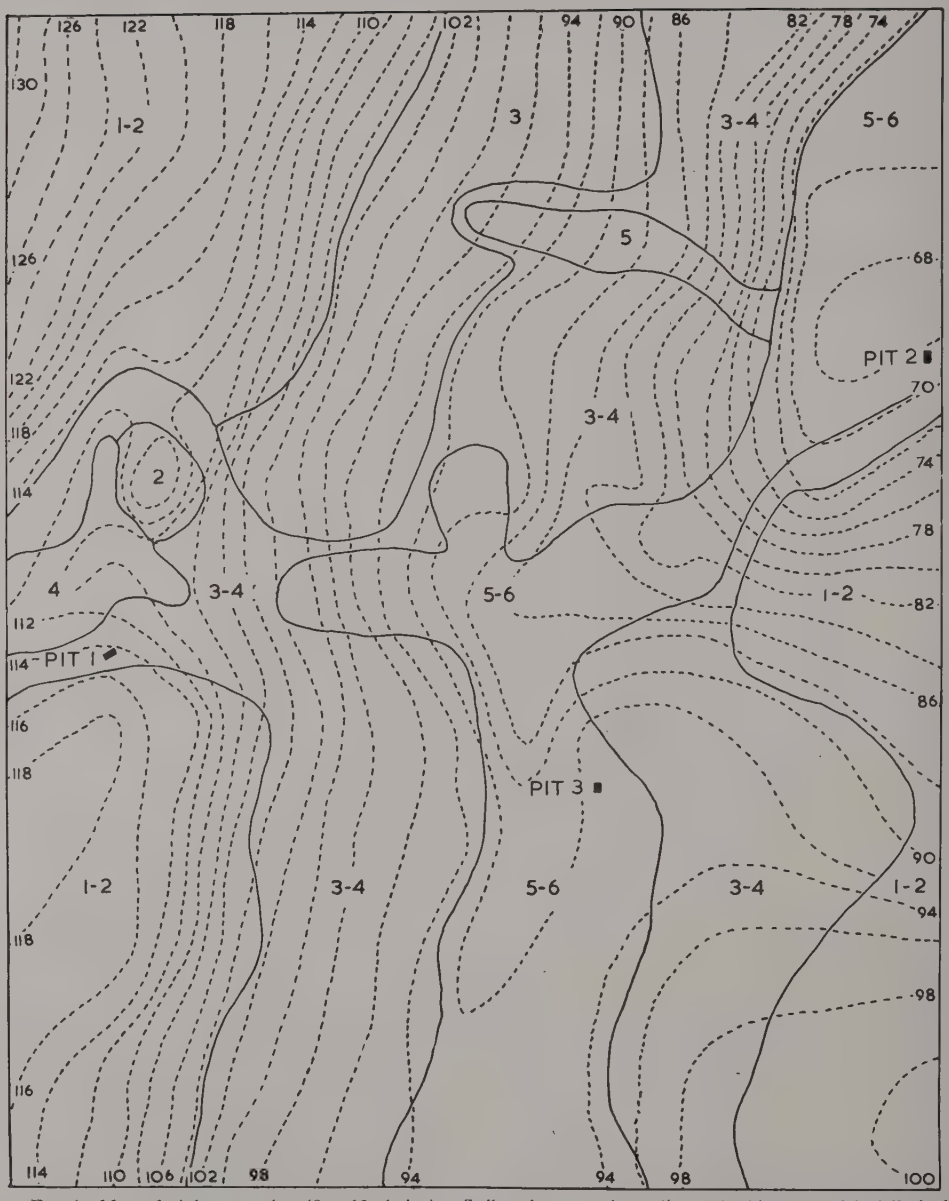

FIG. 1. Map of eight-acre plot (8 x 10 chains). Soil moisture regimes (large Arabic numerals) delimited by solid lines. Contours (small marginal numbers, interval = 2 feet) represented by broken lines. Contour at south-east (lower right) corner of plot arbitrarily chosen as 100 feet.

The A_2 horizon was most acid and had the greatest content of nitrogen, calcium, and magnesium. Potassium content was slightly less than that in the B_2 horizon. The C and G horizons were closer to neutral in their reaction and had the least amount of available nutrients. This gradient in depth is partly explained by the textural analysis which indicates a much larger proportion of silt in the upper horizons and more sand in the lower strata. It appears that the lower deposits had been slightly water-washed following the retreat of the glacier with the resultant

TABLE I. *Description of soil horizons on different moisture regimes*

Horizon	Description	Moisture regimes		
		1-2	3-4	5-6
A_0	Thickness	¾" - 2"	2" - 5"	5" - 11"
	Colour	Dark brown	Dark brown	Black
	pH	4.6	4.5	4.2
A_2	Thickness	1" - 2½"	2" - 4"	Replaced by A_2G
	Colour	Ashy gray	Dark gray	
	pH	4.1	4.5	
A_2G	Thickness	Absent	Absent	2" - 12"
	Colour	.....	.....	Mottled gray
	pH	.....	.....	4.7
B_2	Thickness	3" - 9"	2" - 8"	Replaced by G
	Colour	Choc. brown	Choc. brown	
	pH	5.0	4.6	
C	Thickness	15" - 200"	100" - 200"	100" - 200"
	Colour	Light gray	Light gray	Light gray
	pH	5.5	5.5	5.5
G	Thickness	10" - 20"	20" - 60"	10" - 20"
	Colour	Light gray, brown mottles	Light gray, brown mottles	Gray strongly mottled with brown
	pH	5.0	5.0	4.7
	Distance below surface	108"	24"	12"

TABLE II. *Analysis of the soil horizons removed from Pit 1 located on moisture regime 3*

Horizon	pH	N %	P ppm	CaO %	MgO %	K_2O %	Sand %	Silt %	Clay %
A_2	4.5	0.16	7	0.071	0.013	0.006	..	..	..
B_2	5.5	0.15	2	0.063	0.007	0.007	65	27	8
C	5.7	0.03	1	0.022	0.001	0.001	74	18	8
G	6.1	0.03	1	0.043	0.001	0.001	81	14	5

N—Total nitrogen.
P—Soluble in sodium acetate solution.

leaching out of the available nutrients. The upper eighteen inches of soil may have been deposited from a later advance of the ice. This theory is supported by evidence of stratified sands at the ten-foot depth.

The soil moisture regimes, in general, followed the contours with the drier sites on the ridge tops and steeper slopes. The wetter sites were on the lower slopes where seepage assisted in maintaining a higher water table throughout the year. Although detailed moisture measurements were made on the different moisture regimes, using Fiberglas units with a portable ohmmeter (Colman 1948), only the position of the permanent water table will be considered at this time since detailed moisture, temperature, and tree radial growth data will be considered in a separate contribution. The appearance of a seepage area (5 moisture regime) cutting across the contours in the northern part of the plot was caused by the underlying bedrock topography.

The water table on the dry site (moisture regime 1-2) was usually at depths greater than six feet. This condition was indicated by the position of the gley horizon at the nine-foot depth. In parts of the plot (in the northwest and southeast corners) where the bedrock occurs within two to four feet of the surface, there is no permanent water table, for the water drains through the soil and off over the underlying bedrock immediately after a rainfall.

Soil moisture regimes represented by indices 3 and 4 are characterized by a higher water table together with under-development in both the A and B horizons. The upper part of the C horizon is modified by the fluctuating water table which causes an alternate oxidation-reduction of the iron compounds (Süchting 1950). This reaction is indicated by reddish-brown mottles in the lighter-coloured parent material forming the gley horizon. The soil profile representative of moisture regime 3 is shown in Table III.

TABLE III. *Description of a representative soil profile in moisture regime 3 (from Pit 1) with data on the depth and constituents of each horizon*

Horizon	Depth	Description
A_{00}	0-1"	Litter of birch and maple leaves with a few white spruce needles; light brown.
A_0	1"-2"	Black mull; well decomposed organic layer.
A_1	2"-2½"	Incorporation of organic and mineral material; gray-black.
A_2	2½"-3½"	Varies in thickness from ½" to 2½"; ashy gray.
B_1	3½"-4"	Transition zone; light brown.
B_2	4"-7"	Loamy sand; dark chocolate brown.
B_3	7"-17"	Loamy sand; yellow-brown; few ½" stones.
C	17"-23"	Loamy sand; light yellow-brown.
G	23"-27"	Compacted coarse sand with incipient hard pan; mottled yellow-brown.
G	27"-60"	Coarse sand; soil aggregates compacted around ferric concretions 1" in diameter; reddish-brown.

The loamy sandy till forming the profile described in Table III included 10 per cent stones 4 to 18 inches in size, angular and rounded, mostly granite and gneiss. Root penetration of the neighbouring trees was chiefly in the upper 18 inches although a few branch roots were found as deep as 38 inches.

The development of the soil profile in the sites represented by soil moisture regimes 5 and 6 is controlled largely by the high water table which prevails through most of the year. The organic material does not decompose as fast as on the better drained sites resulting in gradual increase in depth of the A_0 (organic) horizon. This organic layer ranges from 5 to 11 inches on this site with tree roots forming a tangled mass therein.

Water Table

The fluctuations of the water table were measured in three moisture regimes (3, 5 and 6) with a dipstick as well as Fiberglas soil units (Colman 1948). On the drier sites, the water table was usually below the nine-foot depth. Although the relative position of the water table on various sites is related to the amount of run-off and seepage which is, in turn, determined by contours, depth to bedrock and soil permeability, the actual position is principally controlled by the periodicity of the rainfall (Fig. 2). The water table reaches its highest level after the spring thaw. This vernal position of the water table in the various moisture regimes is especially uniform from year to year. Apparently the melting snows provide a surplus of water which percolates through the soil and seeps away laterally along the water table. If a water deficit in the soil is established later, there is a corresponding drop in the position of the water table, until the next rainfall. This drop is more marked on the drier moisture regimes.

In 1949, the period from June 20 to August 20 (Fig. 2) was very dry with only three rainy days (rain over 1/10 inch). Consequently the water table showed a gradual but steady lowering during that period. On July 10, 1949, there was 1.6 inch rainfall which caused the water table on moisture regime 6 to remain steady. However, since the water table on the drier site (moisture regime 3) continued to drop, it indicated that the rain on that date was insufficient to satiate the hygroscopic and capillary water requirements of the upper soil strata; hence there was not sufficient gravitational water to seep downwards to raise the level of the water table. Similarly on August 11, 1949, when there was 2.2 inches rain, the water table on moisture regime 6 rose from 17 inches below the surface to 10 inches, whereas on moisture regime 3 it remained almost unchanged at 60 inches below the surface; then it continued to drop to 81 inches in mid-September, rising again with a week of rainy weather in the latter part of that month. By the spring of 1950, the water table levels on all regimes had returned to the position in which they were one year previously. Since 1950, observations were also made on the position of the water table on moisture regime 5. The 1950 season had a wet summer with rain occurring almost continuously. This was reflected in the much higher position of the water table throughout that year.

The water table was frequently at the surface in moisture regime 5 in the spring when there was accelerated accumulation of run-off water from adjacent slopes and the ground was nearly saturated at all levels even in the drier moisture regimes at this time of the year.

Ground Cover

The plants of the forest floor included some which can be used as indicators. *Sphagnum* spp., *Onoclea sensibilis* L., *Osmunda claytoniana* L., and *O. cinnamomea* L. are limited to the wetter sites (5-6), whereas such plants as *Oxalis montana* Raf., *Viburnum alnifolium* Marsh., *Trillium grandiflorum* (Michx.) Salisb., and *Mediola virginiana* L. are characteristic of regimes 3-4. *Vaccinium myrtilloides* Michx. and *Aralia nudicaulis L.* are more typical of the drier regimes (1-2).

Tree Distribution

The general relationship between tree species and sites has been described by Hills (1953) and Fraser and Prebble (1949). The data on tree distribution and soil characteristics on the experimental plot at Chalk River have been supplemented with reconnaissance studies (Fraser 1952) in order to represent tree distribtuion over the complete range of soil moisture conditions. The relationship is presented in Fig. 3. The diagram is composed of two sections. The lower section (after Hills 1945) illustrates soil profile development on a loamy sand to a depth of six feet, along the Y axis, and the complete range of soil moisture regimes from extreme dry conditions (Θ) to a state of almost continuous saturation (9) along the X axis. The boundaries between the B_3 and C horizons on the drier sites, and the G and C horizons on the wetter ones are shown by dotted lines since demarcation between these strata is usually not clear. Influence of different ecoclimates and parent materials is not considered here. The upper section of the diagram shows the range of each tree species represented by a solid and/or dotted line. The solid line parallels the range of moisture regimes where the species is usually found, whereas the dotted line indicates where the species occasionally occurs under certain conditions.

The climatic climax species have a wide range of moisture tolerance (Fig. 3) as well as that of light. White pine is not considered as a climax constituent since it usually cannot compete successfully with hardwood species on sites with adequate nutrients and moisture. Tree species are considered mesophytic when they have wide site tolerance but are only present in the climax stand in small numbers. Other species include those which are pioneers after disturbance of a mature stand by fire, insects, or other causes.

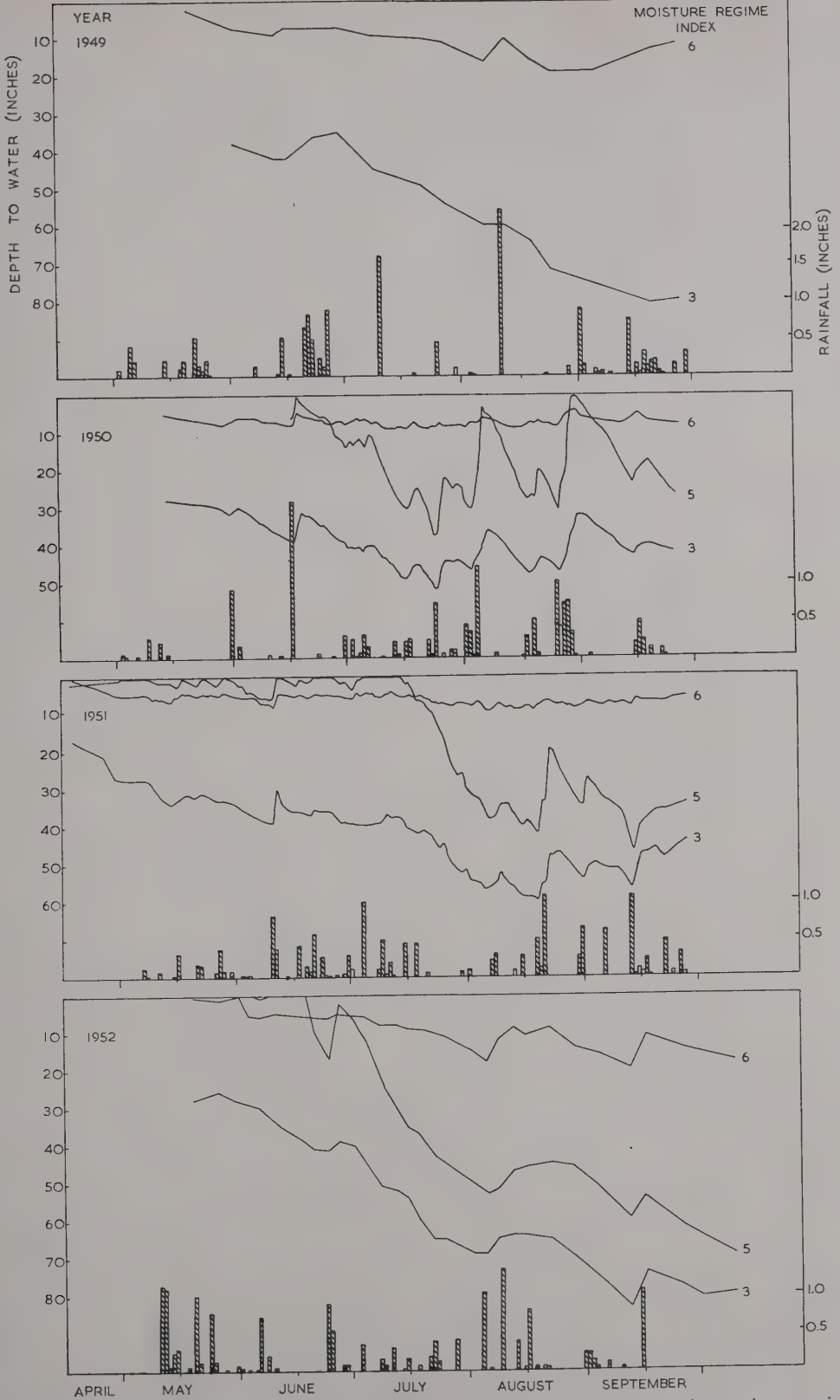

FIG. 2. Graph showing rainfall (histograms) and fluctuations of water table on various moisture regimes for 1949-1952 on the experimental plot at Chalk River.

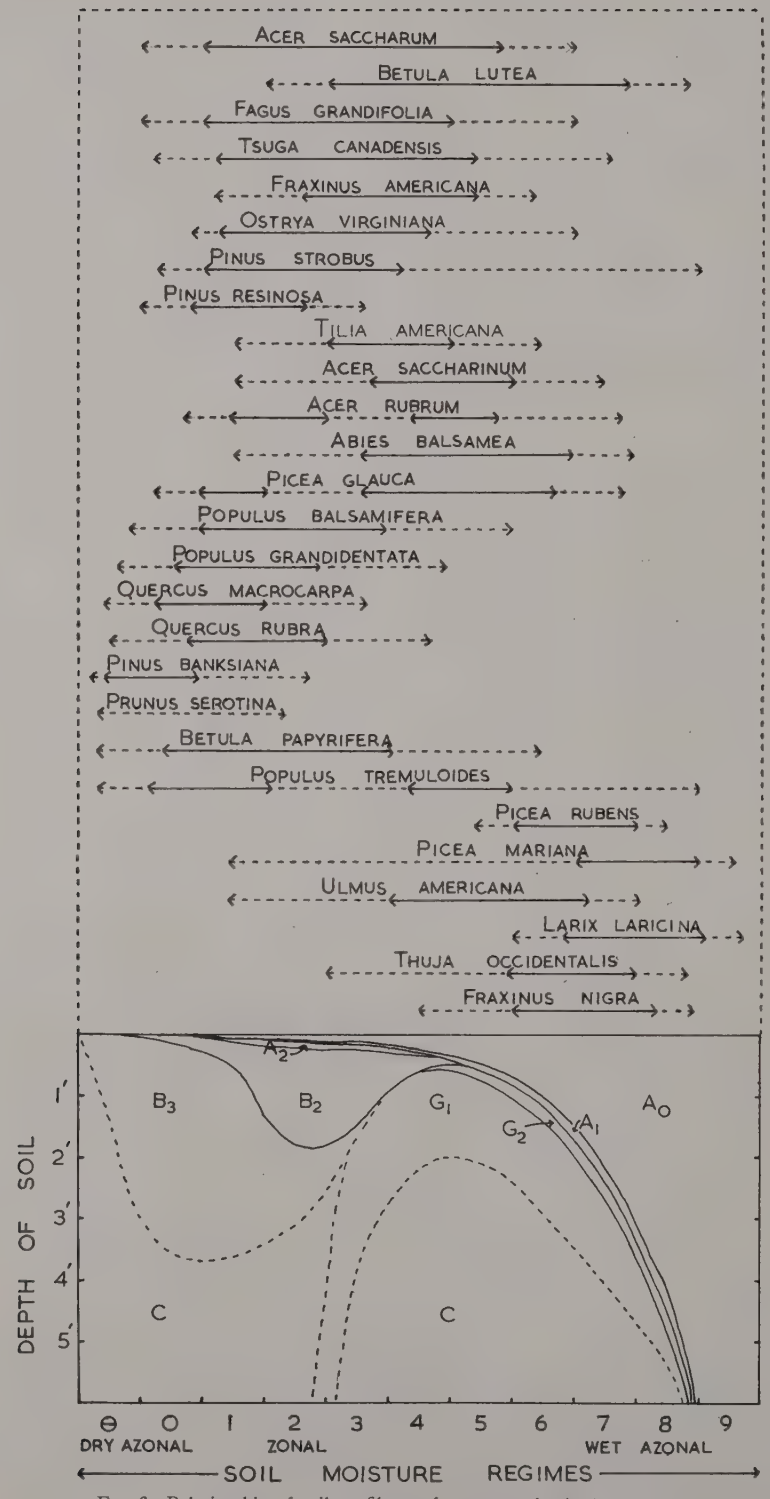

FIG. 3. Relationship of soil profiles to forest trees in the brown podzolic zone of Ontario.

This group includes jack pine, white birch, and aspen poplar which may form an edaphic climax on drier sites. Several species including black spruce (*Picea mariana* (Mill.) B.S.P.), tamarack (*Larix laricina* (Du Roi) K. Koch.) and black ash (*Fraxinus nigra* Marsh.) are more typical of swampy conditions. White cedar (*Thuja occidentalis* L.) is usually found in wetter areas but may occur on drier sites with a high pH.

The distribution of tree species over the experimental plot provided detailed information on moisture preferences. In making a census of trees, a strip one half-chain in width along the boundaries between moisture classes was marked off and the trees within these intermediate zones were not included. The area that remained within each soil moisture class was then considered to be relatively free of interference and therefore satisfactory for analysis of tree species distribution in relation to moisture regime. The procedure followed was to tally trees four or more inches in diameter on the various soil-moisture classes. The number of trees and their basal area are recorded in Table IV.

TABLE IV. *Distribution of tree species by soil moisture regimes (Number of trees (No.), and basal area (B.A.) per acre)*

Tree species	In terms of	Soil moisture regimes				
		1-2	3	3-4	4-5	5-6
Abies balsamea	No.	6.3	0.0	1.2	0.0	8.4
	B.A.	0.8	0.0	0.1	0.0	1.2
Acer rubrum	No.	0.4	0.0	4.8	0.0	16.7
	B.A.	0.1	0.0	1.3	0.0	7.6
Acer saccharum	No.	69.7	24.4	36.9	66.7	18.1
	B.A.	33.8	29.8	20.9	19.5	16.6
Betula lutea	No.	5.4	9.8	20.5	66.7	79.5
	B.A.	2.7	11.8	20.7	50.0	55.4
Betula papyrifera	No.	40.7	2.4	15.7	0.0	0.0
	B.A.	17.7	4.8	4.1	0.0	0.0
Fagus grandifolia	No.	76.4	31.8	22.4	0.0	9.8
	B.A.	20.0	8.5	5.7	0.0	4.1
Fraxinus nigra	No.	0.0	0.0	0.0	66.7	86.5
	B.A.	0.0	0.0	0.0	27.4	24.7
Ostrya virginiana	No.	10.3	0.0	7.2	22.2	4.2
	B.A.	1.6	0.0	0.9	1.9	1.0
Picea glauca	No.	3.1	0.0	1.8	0.0	8.4
	B.A.	3.3	0.0	1.1	0.0	6.2
Pinus strobus	No.	3.1	0.0	1.2	0.0	0.0
	B.A.	6.5	0.0	1.8	0.0	0.0
Quercus borealis	No.	7.1	2.4	0.0	0.0	0.0
	B.A.	2.4	3.0	0.0	0.0	0.0
Tilia americana	No.	11.6	26.9	18.1	44.4	9.8
	B.A.	10.1	23.9	15.2	17.6	16.8
Tsuga canadensis	No.	18.3	83.1	51.3	0.0	55.8
	B.A.	19.6	86.1	51.5	0.0	36.6

This stand is mostly one hundred years old with a few of the trees reaching two hundred. Presence of fire scars on these older trees and charcoal in the organic layer of the soil indicate that a fire occurred shortly before the majority of trees in the stand originated. The older trees are located on the wetter sites (moisture regimes 5-6) where the fire hazard was not as great.

Some of the tree species occur on all sites studied on the plot, whereas other species are limited to a few moisture regimes. The climax constituents, yellow birch, sugar maple, beech, and hemlock occur on almost all sites of the plot. Their root distribution, ascertained from soil pits, appeared somewhat adaptable to the various sites. It is rather deep (18 to 38 inches) and widespread on the drier sites and near the surface (0 to 10 inches) on the wetter sites. However, each of these four species showed a preference for certain sites as evinced by their abundance. Yellow birch frequency increases from 5.4 trees per acre with a basal area of 2.7 square feet on moisture regimes 1-2, to 79.5 trees per acre with a basal area of 55.4 square feet on moisture regimes 5-6. Sugar maple and beech showed a reversed trend to that of yellow birch with greatest abundance occurring on moisture regimes 1-2. Basswood (*Tilia americana* L.) and hemlock on the other hand, were most abundant on sites with an intermediate supply of moisture especially on sites of moisture regime 3. White birch and red oak (*Quercus rubra* L.) were restricted to the drier sites (1-3) whereas black ash occurred only on sites of moisture regimes 4-6. The other tree species were not well represented on the plot although red maple (*Acer rubrum* L.) was usually on wetter sites and white pine on drier ones.

DISCUSSION

The distribution, growth, and condition of forest trees under the same regional climate (macroclimate) are related to variations in site, especially those of soil moisture, soil pore pattern, and geological fabric. In the present study, the soil on the experimental plot was of similar parent material but had a considerable range of moisture conditions. This was evident from the different positions of the water table on the various moisture regimes, and was reflected in the development of the soil profile on different parts of the plot. Fluctuations of the water table were considerable both during the same year, and from one year to another. Concerning the variations in the occurrence of tree species on the different soil sites, it is probable that regeneration conditions were not suitable for all species when the stand was originally established. It is apparent that yellow birch, sugar maple, and beech have a much wider tolerance for moisture conditions than black ash, red oak, or white birch. This adaptation to en-

vironmental conditions may only apply to these species when growing on a loamy sand within a limited climatic range. It is known from reconnaissance studies that tree species may be limited to sites with a high water table on the southern fringe of their range, whereas they may also grow on well-drained sites in the northern areas (Fig. 3).

Even though some tree species show a wide tolerance to site types there is an optimum site on which best growth occurs. The sites suited for best growth do not always coincide with the most favourable sites for reproduction of the species. With annual variations in climate there is a corresponding variation in the position of the water table and the availability of soil moisture on the different sites. Coinciding with this condition is a varied response in radial growth of trees. Details concerning this relationship will be considered in a future contribution concerned with radial growth of trees on the moisture regimes described. Such information should be useful in the interpretation of annual rings and their relation to past climatic fluctuations.

Summary

An eight-acre plot was chosen where distribution, growth, and condition of trees could be related to environmental conditions. Soil moisture regimes were delimited according to soil profile development. The fluctuations of the water table were noted on different sites for the 1949-1952 period. Yellow birch, sugar maple, and basswood were found on all moisture regimes occurring on the plot. White birch and red oak were restricted to the drier sites, and black ash and red maple to the wetter ones. Optimum moisture regimes for various trees were assigned by maximum number and basal area of trees per acre. Data from this plot were supplemented by reconnaissance studies to establish the occurrence of tree species over the complete range of soil moisture conditions. Details of air and soil temperature, soil moisture, radial growth, and condition of trees will be considered in a separate contribution.

Acknowledgments

I wish to thank Dr. M. L. Prebble, Chief, Forest Biology Division, Department of Agriculture Canada, Dr. H. B. Sifton, Head, Department of Botany, University of Toronto, and colleagues of the Forest Insect Laboratory, Sault Ste. Marie, Ont., for their helpful advice. The plot at Chalk River was established by M. L. Prebble, N. D. Martin and the author in May, 1949, in connection with investigations of the condition of yellow birch in Ontario. Mr. Martin assisted in the basic mapping of the plot and accumulated most of the growth data and records of physical conditions during 1949.

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NOTES AND COMMENT

A TECHNIQUE FOR INTRODUCING RADIOACTIVE ISOTOPES INTO TREE STEMS[1]

Techniques for introducing dyes, poisons, and radioactive isotopes into tree stems have been described by Morris (1951) and Fraser and Mawson (1953). Another method has been developed which has proved to be very satisfactory for making a number of applications of radioactive material where speed, simplicity, and a minimum of contaminated apparatus are desirable.

The isotope solution is adjusted to the desired pH and so diluted that the required amount of activity per application is contained in each ml. Each 1 ml. unit is then placed in a shell vial 25 mm. long, with a 12 mm. outside diameter. The vials are stoppered with no. 3 corks, which are barely small enough to fit them. The diameter of the larger end of these corks is 14 mm. A wooden block with a number of 13 mm. (½") holes, 22 mm. (⅞") deep, makes a convenient carrying device when several vials are involved.

At the desired location on the tree trunk or branch, a 13 mm. (½") hole is bored, with a slight upward slant toward the center of the stem, to a depth of 50 mm. (Fig. 1). On rough-barked trees, such as pine, most of the dead bark should be cut away before boring. One of the prepared vials is placed in the hole and its cork seated firmly. Then a dissecting needle, fixed securely in a hand-vise, is forced through the center of the cork; and the vial is pushed off the cork inside the tree. By holding the cork in place with a screw driver, the needle can be withdrawn. The cork and its surrounding area are immediately covered with a sealing substance. A 1:1 mixture of grafting wax and mineral oil makes a satisfactory, easily worked sealer.

The advantages of this technique are as follows:

1. Handling of the exposed radioactive isotopes can be done in the laboratory with maximum convenience, accuracy, and safety.

2. Applications of uniform volume are facilitated.

3. The upward slant of the hole causes the isotope to be concentrated in the region of the phloem, cambium and sapwood whence it is most readily translocated.

4. Suberization is kept to a minimum in that no part of the hole has time to become dry. Air-locks, if formed, do not seem to prevent translocation of the isotopes.

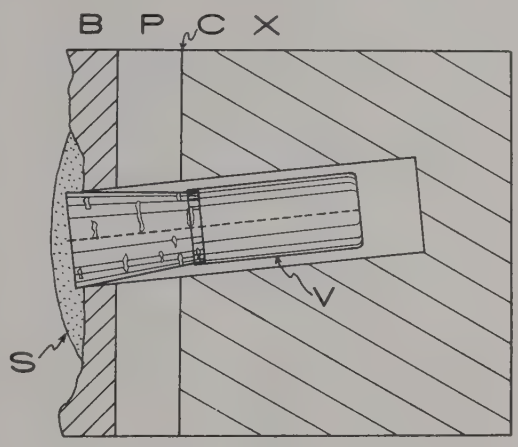

FIG. 1. Radial section through application site showing position of vial before needle is introduced (along the path indicated by the dotted line), to push it off the cork. The wax sealer (S) is not applied until after the needle has been removed. V = vial, containing isotope; B = corky bark; P = phloem; C = cambium; X = sapwood.

5. The basic technique is easily adaptable to situations requiring the introduction of larger or smaller volumes of material.

[1] This work was done in connection with a project financed by contract AT-(40-1)-1031 with the United States Atomic Energy Commission.

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BEN F. GRAHAM, JR.

DEPARTMENT OF BOTANY
DUKE UNIVERSITY,
DURHAM, NORTH CAROLINA

HEXICOLOGY: A NOTE FOR THE HISTORY OF ECOLOGY

If the nineteenth-century saw the birth of many of the biological sciences, the twentieth is the century of their maturing. One index of the developing maturity of any science is its interest in its history, the processes of its development as a self-conscious, unified, and self-contained whole. Although it is possible to point to many intellectual streams and rivulets which contributed to the emergence of twentieth-century ecology, it has not been until recently that that science has come to be regarded—both by its own workers and those in other branches of biology—as a discipline in its own right secure within the much broader and more general scheme of the life sciences as a whole. With this self-consciousness there have begun those first steps in placing ecology within the third dimension of scientific history.

The concise historical introduction of Allee and his collaborators (Allee, *et al.* 1950) has sketched the multiple intellectual currents and the specific contributions—many of them only indirectly related to one another—which contributed so much to the body of data—and some theory—upon which modern ecological concepts are based. This has been no mean task; for certainly none

but the most superficial observers of the natural world, could fail to note here and there the complex web of interrelationships by which the organic world is characterized. Darwin's striking descriptions of the web of life in its specific details was not in any sense unique; it was the theoretical network which he wove about them which reflected his own peculiar genius. In fact, so well recognized was the universality of these interdependencies of species that they formed the major support for the theologically oriented "argument from design" which was so common a biological explanation throughout the last century. Nor in fact could modern biology have arisen were it not for the implicit—and often explicit—recognition of the ecological relationships necessary for so striking a formulation as that of Darwinian evolution. But despite the awareness of these relationships, despite even more, the early coining of the term "ecology" itself, it was left for biologists of the recent past to relate the various strands of theory and data together into a unified field of hypothesis and investigation, upon which peripheral disciplines could draw for insight and stimulus.

Like so much of modern biology, ecology as an investigative discipline is foreshadowed by Darwin's *Origin of Species.* Although never exploited explicitly, the importance of the organism-environment relationship is implicit throughout that work. The *Origin,* as it did for so many other areas of biological research, set the stage for the definition—and consequent exploration—of those problems which have come to comprise the core of modern ecology. But the biology of mid-nineteenth century was still too much hampered by the abstract concept of species to supplant entirely emphasis upon the abstract form or ideal type with one which conceived form only in terms of its relationship with the external world which it inhabited and exploited. As a consequence much of post-Darwinian biology, though operating within an evolutionary frame of reference, held fast to the primacy of form, an emphasis which, incidentally, was strengthened by the introduction of genetics into the evolutionary system.

Where such organism-environment relationships were examined, they represented discrete inquiries, relatively unsystematized and without reference to any particular body of theory.

Lost, however, in the excitement of the inductive demonstrations of evolution's validity, there is the suggestion for a full-blown ecology by one who, as both scientist and philosopher, pursued that wispy unity in nature which was the ideal of the eighteenth-century naturalists. Few biologists have heard the name St. George Mivart —or if they have, they may recall him only as a stubborn, theologically-oriented critic of Darwinism, one of those for whom Huxley reserved his sharpest barbs. Had his influence been greater, however, Mivart might well be regarded as one of the founders of the field of ecology; for certainly, though the lesser known today, he laid the theoretical base of that field and recognized its significance much more explicitly than had his philosophical antagonist, Haeckel, a few years earlier.

Mivart was born in London in 1827; and, like Darwin, whose friend, admirer, and, later, critic he was, he was a self-taught biologist having moved from the law to science, whose study he considered "the highest aim of rational man." An excellent comparative anatomist and systematist, he was also an evolutionist. As a loyal Roman Catholic, however—one of those who joined the Church in the early days of Newman and the Oxford Movement—the philosophy which sustained him as a Catholic made it imperative that he oppose the philosophical implications of Darwinism in whose over-elaboration, he felt, lay the modern fall of man. And though he maintained his position as an evolutionist throughout his life, he felt it necessary to attack continually—most effectively in his *Genesis of Species* of 1871—what he considered the fallacies of the Darwinian statement. It was this sometimes vitriolic conflict with the Darwinians which led in great part to his neglect in the history of science. In the face of the subsequent successes of Darwinism, few read Mivart today except in the spirit of antiquarian interest.

As both a biologist and philosopher, however, Mivart had vision; and as a dedicated theist and philosophical realist, he constantly sought the synthetic basis of universal existence, the broad plan of relationships and of design, which, to him, governed not only the creation of the natural world but its operation as well. It was out of this deep craving for some universal synthesis that he suggested his ecology, though he exploited only superficially his own suggestions.

As early as 1875, in a letter[1] to his publisher, John Murray, regarding the possibilities of a book he was then contemplating, Mivart saw the ecological approach as equal in importance to such other recognized investigative categories as physiology, histology and comparative anatomy. The book was to be a, *"Zoology of Man* attractive to all interested in Man so considered whether or not they care for the anatomy of other animals." And in addition to the comparative anatomy of man (a subject which he had treated in his *Lessons in Elementary Anatomy* two years earlier), the proposed work was to be, "much more full and complete . . . including physiology, histology, races of man, *his relation to time and space and to plants and other animals as his food or his enemies."* (Emphasis added).

This book, the first of a two volume set on mammals, was never published; but six years later the second volume, a mammalian anatomy with the cat used as the representative of that class, appeared with Mivart's ecological approach already developed and ready for application.

Just prior to the publication of *The Cat,* however, Mivart, in a series of semi-popular articles appearing in the *Contemporary Review,* had spelled out the limits and the significances of this new branch of biology to which he gave the name, hexicology.[2] In this charming series on natural history, Mivart sought to demonstrate for the layman the unity which underlay the seemingly disparate specializations which were then slowly becoming synthesized into the science of biology. Three of these articles were devoted to various phases of hexicology. And in these three there is no hesitancy in establishing the position that no proper understanding of the various organic forms can be obtained without first an intensive investigation in and understanding of the environmental unity within which they exist. "Different animals and plants," he wrote, in describing the geographical factors in variation (Mivart 1880a), "are obviously influenced as to their extent of range by the requirements of their several constitutions. . . . Heat, light, moisture and other such influences play evidently an important part in placing restrictions upon organic distribution." He argued

[1] Unpublished letter in the possession of Sir John Murray, London, England.

[2] Mivart coined this word from the Greek "hexis" meaning ("habit, state or condition." The Oxford Dictionary, in ascribing the word to Mivart, primly notes, however, that to be lexically correct the word should be "hexiology."

for further understanding of the biospheric web when he continued that probably, "besides such influences . . . other more obscure causes, probably climatic, affect the existence of creatures in certain localities in ways hard to understand."

It was in the last article of the series (Mivart 1880b), however, that Mivart was most successful in laying down the kinds of ecological relations and details of interdependence upon which a science of hexicology could be based. Having already recognized the importance of the organism-environment relationship for an understanding of a particular form, he analyzed the kinds of relationships which could be observed in the organic world. These "inter-relations of living creatures, as enemies, as rivals, and as involuntary helpers," he grouped "in twelve sets of inter-actions, seven of them favorable and five unfavorable."

1. Thus, in the first place, one kind of organism may benefit another by serving that other as food.
2. One living creature may benefit another by destroying direct enemies of that other, which if not destroyed would prey upon it.
3. An organism may benefit another by destroying indirect enemies of that other—that is by destroying rivals which tend to starve out, though not directly, to injure the organism thus helped.
4. One living creature may benefit another by involuntarily carrying it about, and so serving it as a vehicle for change of place.
5. One animal sometimes benefits another organism by involuntarily feeding it in the process of feeding itself or otherwise.
6. One organism may serve another species by carrying its eggs or seeds which thus become more widely dispersed.
7. An organism of one kind may benefit another organism by accidentally aiding the reproductive processes of such other organism—as insects aid many plants by their visits to their flowers.

As to unfavorable action of some living beings on other creatures:

8. One organism may injure another organism directly, by preying upon and devouring it.
9. It may injure by continuously living with it as a parasite.
10. It may injure it by rivalry, by appropriating its food, and consequently by starvation.
11. It may injure another by benefiting accidentally the enemies or rivals of such other.
12. Lastly one organism may injure another by hindering its reproductive process.

If one takes this analysis of relationships as a working model for investigation, along with the previous statements with reference to the organism's relationships to time and space, it becomes theoretically possible to arrive at a definition of an organic form in terms of his ecological setting, a definition which Mivart considered quite separate from that obtained through anatomical, physiological, or histological research although all such research was necessary for a complete biological definition of the organism involved. In a sense, Mivart, in extolling the hexicological/ecological approach was protesting against the intense drive for specialization which was then becoming apparent within biology, a trend which could lead to the same dangerous compartmentalization of concepts with which natural science had been burdened a century before. Mivart's hexicology was designed more or less to provide those unifying concepts which could systematize all of biology as an investigative field.

In *The Cat*, which was designed as, "an introduction to the study of backboned animals," Mivart did devote a summary chapter to the hexicology of that animal; but so superficial was his treatment and so extensive the limits laid for that field (*i.e.*, he included paleontology), that a reviewer (Anonymous 1881) could justifiably complain that, "we are sure that most readers are comforted to learn that hexicology is a science; but how parasites, extinct allies of the tribe, geographic distribution, and the influence of the phenomena of nature, can hang together in scientific relation, is not much clearer after Prof. Mivart's exposition than it was before."

It is just this lack of discrimination leading to confusion, so characteristic of much of Mivart's thinking and writing, that inhibited the acceptance of hexicology as a self-contained discipline capable of defining and solving problems apart from those inherent in other branches of biology.

Mivart, however, despite this lack of acceptance, constantly maintained the existence of such a field. In one of the last of his general works, *The Groundwork of Science* written in 1894 six years before his death, as an epistemological synthesis, he referred again to hexicology as a special biological science and, cognizant of the criticisms of vagueness, he redefined it as that science "devoted to a study of the relations which exist between organisms and their environment as regards the nature of the localities they frequent, the temperatures and amounts of light which suit them, and their relations to other organisms as enemies, rivals, or accidental and involuntary benefactors." This definition, recognizing the value of the environmental niche in biological investigation, is essentially contemporary in its conception. But by the time of its formulation the stream of biology had flowed away from Mivart, leaving him alone and unheeded, still searching for that universal synthesis in which lay truth.

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Jacob W. Gruber

Department of Sociology and Anthropology,
Temple University,
Philadelphia 22, Pennsylvania

A PRELIMINARY REPORT ON AN EXPERIMENT TO PREVENT CATTAIL DIE-OFF

The death of vast stands of cattails (*Typha*) in the marshes bordering the west end of Lake Erie presents a problem to the managers of waterfowl and muskrat habitats. A study of some of the ecological factors involved in the cattail die-off, was made in the summer of 1952 in the W. E. Levis marshes in Erie County, Ohio, as part of a survey conducted by the Ohio Cooperative Wildlife Research Unit.

This survey indicated that the die-off progressed inland from open water over a period of several years. The cattail shoots at first became thinner (fewer stalks per rhizome) and finally failed to produce shoots above the water. In all cases the die-off was correlated with a high population of carp (*Cyprinus carpio*), and in many cases with a high population of muskrats (*Ondatra z. zibethica*), the latter feeding on new sprouts from the rhizomes in the spring, summer and fall. In the substratum of the die-off areas, there were many channels from one to two and one-half feet deep. It was also noted that the die-off was correlated with a fluctuating water level.

The effect of these and other factors were not analyzed completely, but it was hypothesized that cattail die-off might be inhibited if a fence were built that would exclude carp and perhaps muskrats. Accordingly a fence was constructed in the Levis marshes in May, 1953. An oval enclosure was made of one-half inch mesh hardware cloth containing approximately 11 square yards. The site was chosen at random in an area where some abnormality in cattail growth was evident in the summer of 1952. (See Fig. 1.)

On August 7, 1953, the effect of the fence was evaluated with the following result: the cattail stalks within the fence were taller (9 feet) and more abundant than those in the immediate surrounding area which were shorter (4 feet) and thinner. (See Fig. 2.)

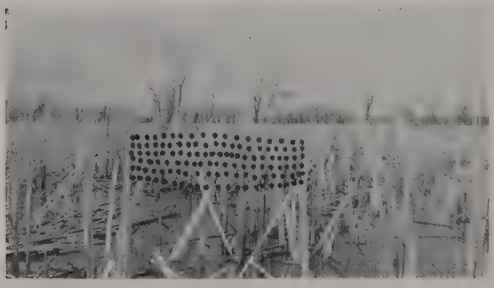

FIG. 1. The position of the fence constructed in May, 1953, is indicated by dots.

FIG. 2. Close up of fenced area on August 7, 1953. Note increased growth within the fence (indicated by dots) as well as the abnormality of cattails surrounding the fence.

It is our belief that the die-off of cattails is due primarily to a combination of carp and muskrat activities and possibly other animals, such as snapping turtles (*Chelydra serpentina*) and the gizzard shad (*Dorosoma cepedianum*). It appears that the muskrats crop all new shoots during the growing season which cuts off the food supply to the rhizomes. The foraging and mating behavior of the carp apparently undermines the rhizomes and presents new growth to the muskrats. The water level becomes an important factor in die-off since it governs the limits of the activities of the carp. In addition, the fluctuations in the water level result in increased foraging of the area by the carp.

More experimentation is desirable before all factors are correlated and the practicality of fencing is determined. It appears that a fence of larger mesh might reduce the cost without losing its effect. It is also possible that well spaced fenced areas might permit stands of cattails at the outer limits of die-off areas and eventually result in channels and open areas which are desirable from a wildlife managerial standpoint.

M. L. GILTZ
W. C. MYSER

DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY,
THE OHIO STATE UNIVERSITY,
COLUMBUS 10, OHIO

COMPETITION AS A POSSIBLE LIMITING FACTOR IN THE DISTRIBUTION OF *MICROTUS*

In attempting to define the factors delimiting the ecological or geographical distribution of any organism, the physical factors of the environment, climate, availability of suitable nutrition, geological history, and biological competition are among the factors properly to be considered. Competition often takes place between closely related species since their ecological requirements are apt to be similar. Some differences in ecological requirements are thought to be necessary for the sympatric existence of two closely related species. The geographical and ecological distribution of three American species of the mammalian genus *Microtus* seems to illustrate these points.

Microtus pennsylvanicus, the meadow vole, occupys an extensive range in the eastern United States, in Canada, in the northern Great Plains, and in the Rocky Mountains. *Microtus ochrogaster*, the prairie vole, occurs throughout the Great Plains from Oklahoma northward, eastward to Ohio and westward to the foothills of the Rocky Mountains. *Microtus montanus*, the mountain

FIG. 1. The ranges of three species of *Microtus*. Solid line encloses the range of *M. ochrogaster;* dashed line encloses the range of *M. montanus;* line of circles encloses the range of *M. pennsylvanicus*.

vole, occurs in the mountains of the western United States northward into south-central British Columbia (see Fig. 1).

Throughout much of its range east of the Mississippi River, *M. pennsylvanicus* is ubiquitous, occupying swamps, meadows both wet and dry, and even forested areas. Thus, Hamilton (1943: 325) in speaking of this species states: "Every conceivable niche supports a few, . . . Indeed, few mammals are so widespread or found in such a wide variety of habitats." In the north, particularly in areas where it is not confronted with a competitor of the genus *Microtus,* it occupys the same latitude of habitats. Speaking of this species in the plains area of southern Saskatchewan and southeastern Alberta, Soper (1946: 147) states: "Diversity of habitat is also remarkable, ranging from the heavy coniferous woods of the Canadian Zone to the shortgrass-sagebrush plains of the Upper Sonoran Zone." In much of this region *Microtus ochrogaster* is absent, although it is locally abundant in southeastern Saskatchewan and farther east. In Glacier National Park, Montana, meadow voles are, according to Bailey (1918: 63), rather generally distributed in open grassy areas, and are "sometimes found in wet marshes and along the margins of streams and lakes." Here neither *M. ochrogaster* nor *M. montanus* occurs. In northern Idaho, according to Rust (1946: 321), the meadow vole "prefers grassy meadows and openings, both marshy and dry, along streams in the Canadian Zone." Again, neither the mountain nor prairie vole occurs in the area in question.

A somewhat differtnt ecological picture is to be seen in those places where the range of *M. pennsylvanicus* overlaps that of *M. ochrogaster.* In this region, but particularly in the more western portions of the range of the prairie vole, the meadow vole is more often than not restricted to wet marshy areas in the vicinity of water. In Dundy County, in southwestern Nebraska, I have collected *M. pennsylvanicus* only in lush swales in the vicinity of water while *M. ochrogaster* is found in the dry grasslands. Throughout its range the prairie vole is known to show a preference for drier areas, although where *M. pennsylvanicus* is rare or absent *M. ochrogaster* is found in wet areas as well (see Cockrum 1952).

Where the range of the meadow vole overlaps that of *M. montanus,* somewhat the same situation prevails with the mountain vole assuming the role of *M. ochrogaster.* In northwestern Wyoming, *M. pennsylvanicus* seems to be restricted to wet hydrosere communities while being rare or absent in drier grasslands where the mountain vole in abundant (Findley 1951). *M. montanus,* on the other hand, is uncommon in hydrosere communities when the meadow vole occurs in them. In Colorado, Warren (1942: 228) says of *M. pennsylvanicus*: "The Saguache vole prefers to live about damp and marshy places . . ." while *M. montanus* ". . . seems to prefer drier ground than the Saguache vole, and is found much on the grassy hillsides; at the same time it is found in the meadows."

In areas where the meadow vole does not occur, as in Nevada, the mountain vole occurs regularly in wet places (Hall 1946: 542). Furthermore, in areas within the range of both *M. montanus* and *M. pennsylvanicus* where the latter is excluded because of altitude, the former also occurs in hydrosere communities. Such a situation may be observed in certain high mountain areas in Colorado (Findley and Negus 1953).

When the above data are analyzed, we emerge with certain tentative conclusions regarding the causes for the relative ecological distribution of these three species of *Microtus*:

1. Where *Microtus pennsylvanicus* occurs by itself it is capable of occupying most available habitats including both wet and dry grasslands and even the dry sage-grasslands of the northern plains. This is true of both *M. orchrogaster* and *M. montanus* except that neither regularly inhabits woodlands.

2. Where the range of the meadow vole overlaps that of *Microtus ochrogaster*, a species seemingly best adapted to dry prairie grasslands, the meadow vole is forced to retreat to its optimum ecological niche, namely moist marshly areas near water.

3. Where the range of *M. pennsylvanicus* overlaps that of *M. montanus*, a species well-adapted to existence in dry mountain grasslands, the meadow vole is again forced to retreat to its optimum niche, the hydrosere community.

4. The meadow vole may be thought of as typical of the eastern deciduous and northern coniferous forests and their attendant grasslands. As it approaches the southwestern periphery of its range this vole becomes more and more restricted to hydrosere communities. This is due, in part at least, to competition with closely related microtines.

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James S. Findley

Museum of Natural History,
University of Kansas,
Lawrence, Kansas

NORMAL FIELD MOVEMENTS AND GROWTH RATES OF MARKED REGAL HORNED LIZARDS (*PHRYNOSOMA SOLARE*)

Individuals of a local population of the regal horned lizard (*Phrynosoma solare*) have been captured alive, measured, permanently marked (clipped toes), and released exactly where found, during and since September, 1950. The population is located approximately four miles north of Tucson, Arizona, at, and in the vicinity of, 2103 East River Road, at the foot of the bajada of the Santa Catalina Mountains, along Rillito Creek. The study area of approximately one acre extent is not cultivated, gardened, nor greatly disturbed, and is occupied by the following species of lizards: *Callisaurus draconoides, Urosaurus ornatus, Sceloporus magister, Phrynosoma solare,* and *Cnemidophorus tigris.* Individuals of all of these species have been marked and released. The principal plants are palo verde (*Cercidium microphyllum*), mesquite (*Prosopis juliflora*), creosotebush (*Larrea tridentata*), bur sage (*Franseria deltoidea*), ocotillo (*Fouquieria splendens*), arborescent chollas (*Cylindropuntia*), prickly pears (*Platyopuntia*), and tamarisk (*Tamarix aphylla*), all on gravelly sandy soil.

Of a total of five adult horned lizards marked to date on the study area, recapture data is available for three (1 ♂, 2 ♀♀). Table I summarizes pertinent data for these individuals. Animals have been recaptured up to three years after original capture-and-release.

It was suggested earlier (1947) that marking studies of horned lizards in the field should undoubtedly establish a highly sedentary behavior for this life-form which is one of those diurnal terrestrial vertebrates that epitomizes concealing coloration by background matching of dorsal

Table I. *Snout-vent lengths and distances traveled for recaptured horned lizards* (Phrynosoma solare)

Sex, age, and dates	Original S-V length	S-V length upon recapture	Distance from original capture-and-release point	Time since previous capture-and-release	Average distance of travel
Male, adult					
9-18-50	97 mm.	.....	.....	.....	
8-10-51		99 mm.	20 yds.	ca. 1 yr.	
8-3-53		102 mm.	43 yds.	2 yrs.	
					31.5 yds. (28.8 m.)
Female, adult					
9-22-50	80 mm.	.....	.....	.....	
8-17-51		83 mm.	16 yds.	ca. 1 yr.	
8-19-51		83 mm.	19 yds.	2 days	
9-13-51		84 mm.	26 yds.	25 days	
9-9-53		93 mm.	16 yds.	2 yrs.	
					19.0 yds. (17.4 m.)
Female, adult					
9-17-52	86 mm.	.....	.....	.....	
7-20-53		88 mm.	20 yds.	10 mos.	
					20.0 yds. (18.3 m.)
Average distance of travel (N=7)			22.9 yds. (20.9 m.)		

color and pattern concomitant with structural and attendant behavioral adaptations. The present data while limited are consistent and indicate a highly sedentary nature for *Phrynosoma solare*. The mean distance of travel, for each recapture point from the original capture-and-release point ($N = 7$), is 22.9 yards (16-43). This indicates a tendency to remain in a relatively limited area (home range), and one of a probable magnitude of less than 100 square yards, whatever the distances of travel may be over an entire season or several seasons. These data show a similar distance traveled at recapture after two years as for recapture after two days. Moreover, these limited data are consistent with findings that male lizards move somewhat greater distances than females of the same species (*e.g.*, see Stebbins 1944).

These data further disclose a slow annual growth rate (body length) for individuals of this species over 80 mm., snout to vent. Maximum S-V length is this species is ca. 110 mm. (a female). Accuracy in measurement is to the nearest 1.0 mm. for the data given in Table I. The mean annual growth for the two females, both in a size range of 80-95 mm., is 3.4 mm. per annum; for the male, in a size range of over 95 mm., 1.7 mm. per annum.

This relatively slow growth rate appears to be not unlike that for the much smaller and crepuscular-nocturnal *Xantusia vigilis*, the desert night lizard, which is being analyzed by R. G. Zweifel and the author in a long-term ecological study involving large numbers of marked individuals in a section of Joshua-tree forest on the Mojave Desert in California.

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Charles H. Lowe, Jr.

Department of Zoology,
University of Arizona,
Tucson, Arizona

COLLEMBOLA FEEDING UPON NEMATODES

The following observations were made in Melbourne, Australia during the early spring (September) of 1950. A small colony of the dacetine ant, *Alistruma* n. sp. (Brown ms.), had been secured from a rotten log in wet sclerophyll forest at Sherbrooke Forest, Dandenong Ranges, Victoria, along with some of the rotten wood in which the nest chambers had been excavated. The ants and the rotten wood were placed in a small glass-topped plaster observation nest in the course of experiments to determine food preferences of the ants, since related dacetines were known to prey upon furculate collembolans of several families. Conditions within the nest were kept very moist, so that a film of water collected on the under side of the glass, and in this film appeared from time to time slender nematodes of lengths judged roughly to be about 1 to 2 mm. The nematodes showed unceasing rapid undulant or whiplash movement like that of the common vinegar eel. The nematodes also appeared in numbers on dead ants that had been placed on the refuse heap of the nest.

Among other small arthropods, I introduced into this nest several species of Collembola; of these, the form most often used appeared to be the commonest springtail in Melbourne gardens at most seasons of the year. This was an *Isotoma* or a related genus of the Isotomidae, unfortunately not preserved for proper identification. Individuals of this form were often seen walking along the underside of the glass, "grazing" in the film with moving mouthparts and leaving a faint trail in the moisture. When a springtail came upon a nematode, even a worm nearly as long as itself, the worm was on each occasion seized at one end and rapidly and smoothly ingested, although still undulating rapidly until the free tip disappeared. The process of actual ingestion took only two or three seconds once begun, and therefore *appeared* to be accomplished at least partly by some kind of suction produced by the collembolan. The observation was repeated on several (at least ten) occasions, and each time was the same in details of the process. The Collembolans showed no obvious significant orientation toward the nematodes until almost within direct contact range through their only moderately long isotomid antennae. Once antennal contact was actually made, however, the nematode was in each case actually consumed without delay. In seizing the worms, the Collembola appeared to use directly only their mouthparts.

I had planned to continue observations of this behavior of the Collembolans, but other work interfered. It should be possible, however, to test isotomids for nematode feeding habits under similar, easily set up conditions in other parts of the world than Australia. So little is known about the food habits of many Collembolans (and the predators of nematodes) that further investigation might prove rewarding out of all proportion to the slight difficulties involved in making the observations. Action taking place in a small plaster nest on the underside of the glass cover is readily followed even at medium powers of the dissecting microscope in moderate illumination.

W. L. Brown, Jr.

Museum of Comparative Zoology,
Harvard University,
Cambridge 38, Massachusetts

NOTES ON THE PREDATION OF THE HARD CLAM, *VENUS MERCENARIA*, BY THE MUD CRAB, *NEOPANOPE TEXANA*

The predatory nature of the common mud crabs with respect to oyster populations in Delaware Bay has been recognized and noted (McDermott and Flower 1952). However, to the author's knowledge nothing has been published concerning their potential danger to other bivalves.

During 1953 laboratory and field observations were made of suspected enemies of the hard clam. The mud crab, *Neopanope texana*, was considered because of its abundance in hard clam areas under study in Narragansett Bay.

Laboratory Observations

In one experiment carried out during June and early July, 50 hard clams (average length 10 mm) were allowed to dig themselves into the sand bottom in a tank supplied with running water. Five mud crabs (average width 15 mm) were then introduced into the tank. At the end of 30 days, the experiment was terminated and the crabs removed from the soil by screening. Thirty-three of the 50 clams had been broken to the extent that only by counting hinge pieces could the amount of predation be directly determined.

In another experiment during September, 37 set-of-the-year hard clams (1-7 mm in length) were allowed to bury themselves in the sand bottom of a running water tank. Twenty-five clams (15-25 mm in length) were allowed to become established in the sand of a second tank. Three mud crabs (approximately 15-20 mm in width) were added to each tank. In 18 days when the experiment ended, all 37 of the set-of-the-year hard clams had been crushed and eaten. Four of the clams in the second tank had been opened. These had not been crushed; instead, the lips of the valves were chipped as though the crabs only gradually gained access to the soft parts. The victims measured 13, 16, 17, and 17 mm in length.

A third experiment carried out in November gave some information on the predaceous activity of *Neopanope* in relation to lowered water temperature. This experiment was begun in tanks of aerated water at summer temperatures of 20-23°C. Eleven hard clams (1-9 mm in length), and two mud crabs (15 mm in width) were placed in one tank with no sand bottom for the clams to dig into. In the second tank, also without soil, were placed 11 hard clams (14-33 mm in length) and two mud crabs. Within 24 hours, all but one of the clams in the first tank had been crushed and eaten. None of the clams in the second tank had been opened nor was there any evidence of attempt. Aeration was discontinued and the running water supply turned on. In a short time, the water temperature was down to 12.5°C. Thirty hard clams (1-9 mm in length) were added to the first tank. The original crabs were retained. At the end of the next 24 hours, 11 clams had been crushed. At the end of another 24 hours, eight more clams had been destroyed. During the next three days, the remaining 11 clams were crushed and eaten. During this time the water temperature fluctuated between 11°-12.5°C. No evidence of predation in the second tank was apparent at any time during this experiment.

Field Observations

During the fall of 1952, 2,000 set-of-the-year hard clams (2-6 mm in length) were planted in a 6′ x 3′ bottomless box sunk into the intertidal flats in Wickford Harbor, Rhode Island. The object was to measure the growth rate of the clams and the extent of predation by the oyster drills *Urosalpinx cinera* and *Eupleura caudata* which are common in the vicinity. Coarse mesh hardware cloth was used as a cover to exclude the blue crab *Callinectes sapidus* and curious diggers. In November 1953, the clams were redug. Only 258 individuals were recovered (8-20 mm, average 13 mm in length). In addition, 39 broken and chipped paired shells approximately the same size as the live clams were screened out. Only 13 shells of any size were found with drill holes. Present in the box were 11 *Urosalpinx* and 48 *Neopanope*. The fate of the missing clams can only be a subject for speculation. However, in the light of observations in the laboratory, it is conceivable that mud crabs were a major contributing factor in decimating the planting while the individuals were still very small.

The data presented show that the mud crab is a menace to small hard clams and is particularly voracious in its predations on clams less than 10 mm. in length. *Neopanope texana* is described as common to very common along the whole Atlantic Coast from Prince Edward Island to Florida (Pratt 1948 and Miner 1950). This is practically coincident with the range of the hard clam. If the above observations are typical of *Neopanope* activity, it must be considered a potential enemy to the hard clam throughout its range.

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Warren S. Landers
U. S. Fish and Wildlife Service,
Kingston, Rhode Island

REVIEWS

Permian Marine Paleoecology[1]

Time was when the rocks of west Texas and southeastern New Mexico seemed to offer little more than indifferent semi-arid pasturage. The discovery of oil, a few decades ago, in the Permian rocks deep below the surface revealed the existence of vast wealth in the form of liquid fuel. Since then these rocks have been intensely studied by sub-surface methods over a huge area and by direct observation in the trans-Pecos region where they rise to the surface in the Glass, Delaware, Guadalupe, and other mountains. One result of this concentrated activity has been the revelation of the most magnificent sequence of Permian rocks known anywhere in the world, considered by many to be a suitable world standard because of the completeness of their sedimentary and fossil record. The other result was the development of a curious picture of the regional environment of deposition of these rocks in subsiding deep marine basins with restricted connections with the ocean, bordered by reef structures behind which extended toward an arid land vast lagoons where salt and other evaporites were deposited. One of the basins, the Midland, is known only from subsurface study, but the rocks of the Delaware basin can be examined at surface outcrops. At first the concept of a lagoon-reef-basin regime was only an intriguing hypothesis which seemed best to explain the puzzling differences in rocks of the same age from place to place. The work of many geologists has slowly raised this tentative suggestion above the level of hypothesis through theory to an established fact which can be used as a test area for sedimentological and paleoecological ideas.

This new book is a most satisfactory attempt to present a "systematic, intensive, simultaneous study" of the "sedimentary structures, lithologic character of the rocks (as shown by hand specimens and thin sections), chemical composition, and the characteristics and facies distributions of the fossils." This is based largely on several years' work in the laboratory and field by a geological team under the general direction of Dr. Newell, and in passing we should tip our hats to the Humble Oil and Refining Company for its stringless and considerable financial support. The writers were not content, however, only to study the dead past in the Delaware basin, and turned for illumination on the problem of reef ecology to a personal study of the living reefs of the Bahamas and the South Pacific, with obviously good returns.

The first three chapters are devoted to a thorough analysis of the geologic setting of the Delaware basin, with demonstration of the existence of a barrier reef around the basin grading away from the basin into lagoonal deposits, and into the basin and its euxinic deposits. Here is found a recognition of greater amounts of talus deposits downward from the degradation of the margins of the reef than heretofore allowed. Chapter 4 is a lengthy discussion of the reef complex and its associated sedimentary phases, forming a clear reconstruction of the barrier reef, which shows striking similarity to modern reefs, even to such details as reef channels normal to the reef front, and talus slides down the steep slope from reef into basin. The next chapter is a study of the lithologic changes (diagenesis) after deposition and before surface weathering. "Some modifications are extensive and have obliterated many of the original features of the sediments"—as recrystallization, dolomitization and chertification, and silicification of organic remains, the last of special interest.

Then comes a chapter entitled "Paleoecology of the Permian rocks": the interpretation of the climate, terrestrial topography, submarine topography, hydrography of the Delaware basin, stagnant basin, reef and bank, and shelf environments. The Permian maritime climate of the southeastern United States is considered to have been considerably milder with higher mean temperatures than at present, more like that of the Gulf of Mexico region, but with rate of evaporation greatly exceeding rates of precipitation and stream replenishment. The eastern shore of the inland sea in central Texas may well have received appreciably more moisture early in the Permian. Characteristics of the rocks indicate that the terrestrial topography was "subdued," with no local source of sediments. Submarine topography was pronounced with steep slopes from the barrier reef ring to the floor of the basin with depths down to 1800 feet a couple of miles out from the reef, and with very shallow seas behind the reef. The waters of the basin were aerated at the surface and euxinic below, with evidence of periodic disturbances of the thermocline with overturn of deep waters. Distribution of fossils indicates well-defined ecologic zonation over the area as a whole, with a poor benthonic basin biocoenose, a modest pelagic biocoenose of ammonoids and Radiolaria, a rich reef fauna of algae—the principal reef constructors—fusulines, sponges, brachiopods—especially the famous Tethyan aberrant forms—and many others, and a limited shelf fauna of a few euryhaline types. One might have wishes for more detailed development of these biocoenoses whose biotopes are so fully described, but there still remains much systematic work before the faunal compositions will be fully known.

Technically the book is good, as might be expected, for we are coming to look for good things from Freeman. The diagrams are clear and to the point, mostly new or carefully re-drafted. The 32 excellently reproduced plates include 225 illustrations of air views of the Delaware basin, details of rocks and stratigraphy, photomicrographs of lithologies, and fossils, all carefully chosen to illustrate the text, not hastily selected afterthoughts.

For the stratigrapher there is here for the first time a clear picture of these now classic and stratigraphically complex rocks. For the sedimentologist it is a sound exposé of the sedimentary types encountered in this area and their relations, on which he can ponder, to interpret otherwise if need be. For the ecologist the Permian basin comes alive as an example from the past to compare with the present. If the paleoecologist must continually turn to the living world for clues to the past, may not the ecologist not occasionally look back over his shoulder to add a third dimension—time—to his viewpoint? If so, he can profitably peruse this book.

John W. Wells

Department of Geology
Cornell University

[1] N. D. Newell, J. K. Rigby, A. G. Fischer, A. J. Whiteman, J. E. Hickox, and J. S. Bradley 1953. *The Permian reef complex of the Guadalupe Mountains Region, Texas and New Mexico.* 308 p., 32 plates, 85 text-figures, incl. 4 folding charts. San Francisco: Freeman and Co.

Another Speculation on Reality[1]

A book of this title, appearing under the imprint of the Philosophical Library of New York which includes listings by such authors as Albert Einstein, John Dewey, George Santayana and Alfred North Whitehead, will attract the serious attention of all interested in the philosophic foundations of modern science. In this instance the publisher gives us no information concerning the author; he is credited with no affiliation on the title page; and the author in his preface refers only to "fifty years of technological practice." Author Laucks is a chemist, a septuagenarian, who has been in the commercial field since the age of 22. He has been president or director of various organizations in the field, no less than ten of which bear his name. He admits that these first fifty years had given him "a strongly materialistic viewpoint. However, as . . . [his] knowledge of the psychic field increased, . . . [he] came to the conclusion . . . that psychic phenomena constitute just as real a part of the world" as his chemical reactions. In this respect, Mr. Laucks follows a pattern that is extremely frequent in minds far greater than his or mine. Increasing age gives changing outlooks, and these are attributed to various factors which neither psychologists nor physiologists have adequately considered.

The greatest urge at any age is a satisfaction of that curiosity as to the what and the why of the universe. Some just wonder; others find ready-made answers in the various theologies; and the eclectics search and search and come up with their own variant cosmology. With modern printing, coupled with the urge of many to write, cosmologies are now available at bargain-basement quantities and rates, designed to fit almost every intellectual size and shape. Mr. Lauck's cosmology is ideally suited for those who have a very materialistic leaning, who do not want much mathematics, who have no inclination to grapple with the contortions of logic, epistemology and metaphysics, and who disdain the occult and the esoteric. The author, taking the basic form of a simple chemical equation undoubtedly learned as a youth and comfortably engrained through the years, has by analogy and by mental legerdemain interpreted the whole universe in its terms. The result is a remarkably "neat" and uncomplicated cosmology that will be acceptable to many scientists, and most certainly to those who have lived with chemistry.

In the Introduction we are confronted with the basic problems: the nature of the universe, Reality, matter, energy, and "consciousness and soul." He answers many of the problems then and there. Reality, by definition, is that which constitutes the universe. Reality cannot be "matter," for matter is really energy (he so wishes to use the equation $E = mc^2$). Since he chooses to accept "consciousness and soul," it must be Reality, therefore it must be matter, therefore it must be energy. Thus we end up with a huge universe just of energy, a bit of which easily carries us through the rest of the book.

Chapter 1 is a compressed survey of modern physics, good as a review, but tough going for one without a college course. Chapter 2 is a parallel survey of chemistry. In Chapter 3, "Life as a Chemical Reaction," the phenomena of life are considered as biochemistry. The origin of life is made to sound plausible in terms of the origin of proteins. Then viruses are discussed as similar to protein molecules, which constitute genes. Finally the origin of the first living cell is credibly described as the result of reactions between mixtures of proteins.

Chapter 4, "The Basic Processes of Aggregation and Dispersion" is the most critical of the entire book. In it, the author notes that "the whole universe can be attributed to the interplay of . . . two basic tendencies —aggregation and dispersion . . ." This is nothing more than saying that in a universe which is not "dead," any movement action or other phenomenon must be either to, or away from, something else. Actually, the idea can be linked readily to the basic chemical formula, which is a reversible endothermic or exothermic aggregation of matter. The diagram on page 69 is the heart of the book, for here Mr. Laucks puts all known phenomena of the universe in terms of reversible aggregations of matter (bound energy), and incoming and outgoing radiation (loose energy), each such aggregation with a "nimbus" that unites by analogy an amazing variety of such otherwise unrelated unknowables as soul, life, gravity and cohesion. There are two sequences. One starts with unknown nuclear particles, and progresses through nuclei, to molecules, bulk matter, planets and stars. The other starts with C, H, O, and N, and progresses through amino acids, proteins, genes, cells and man. The two series are connected by interchanges of radiation. In short, the basic pattern of a chemical formula is found adequate as a device to comprehend all normal phenomena of the universe.

"Life" now takes the stage. In Chapter 5, "The Relation of Evolution to Chemical Reactions," the subject is briefly so discussed. Next in line (Chapter 6) are instincts, tropisms and reflexes, handled similarly as "The Relation of Instincts to Chemical Reactions." I fully expected that the following subject logically would be "intelligence," but it is quite amazing that intelligence neither receives a chapter, nor is the word used more than a few times in the entire book. Instead, the author jumps from instincts directly to (Chapter 7) "How the Soul Develops." Perhaps the word soul here only causes semantic confusion. Its use may satisfy some early religious training of the author, but it would satisfy no serious churchgoer. His is certainly the most materialistic soul I have ever known: it is constantly identified in terms of communications (voice organs) and manual dexterity (hands). A soul is something that is developed in the life of an individual. "Even the fondest mother will agree that a new-born baby has no soul." Thus, it is to be identified with what most of us would call the actual acquirement of our cultural heritage—not even the ability for that requirement. In this respect, he identifies it with an individual's "intelligence," defined, not as an ability, but as "the knowledge which he gradually acquires from infancy to old age." Mr. Lauck's soul appears to be nothing more than his learned knowledge.

It is essential to the author's thesis to recognize all phenomena as "real" and thus we are not surprised at his handling of that which lies beyond the soul (Chapter 8), as "The Reality of Psychic Phenomena." "That these phenomena do occur is attested by such a mass of evidence that any open-minded reasonable man must accept their truth." With surprising gullibility, he considers telepathy, precognition, clairvoyance, even levitation and ectoplastic materialization, as well as faith healing and other religious phenomena. He finds that scientists now "have placed the above phenomena on the same footing as those dependent on the Second Law of Thermodynamics." He recognizes charlatanry in the

[1] Laucks, Irving F. 1953. A speculation in reality. 154 pages. New York: Philosophical Library. $3.75.

field but relates that "Such performances however have no relation to experiments carried out under carefully controlled conditions. In the works cited there are records of hundreds of such tests carried out by eminent scientists. It is impossible for on open mind to reject such an array of evidence." We anticipate Chapter 9, "A Speculation in Reality" as a plea for the independence and permanence of the soul, and as an interpretation of psychic phenomena, all in terms of chemical equations. We are not disappointed. In untrammeled speculation, and without ever mentioning "immortality," Mr. Laucks considers the soul as a higher non-material type of aggregation (bound or fast energy), which both broadcasts and receives what he calls A-waves (loose energy). Only a very few of us are capable of receiving and interpreting these A-waves, and it is those few who are the psychics, the mystics, and sometimes even the dictators, among us. In concluding Chapter 10, "What of It?", the materialist continues to predominate. Problems in religion, politics and medicine are related to a better understanding of this material yet immaterial soul, and its A-waves. He ends with a wish for another organization like the Rockefeller Foundation, for research on the soul. I am tempted to suggest its slogan be "Harness the A-waves!' And then I am confronted with an appalling thought. We do not have souls at birth. Souls are only individual stores of accumulated knowledge, becoming separate and permanent after death, bombarding the universe with A-waves that are independent of space and time. To become receptive to these A-waves of almost infinite accumulations of the knowledge of all dead men and other animals might fill the lost pages of history. Unless however at the same time we develop some selectivity ("Calling Cleopatra! Cleopatra *only* please answer."), the assault of loose-energy messages from such fast-energy souls would reduce our present human mind to a shambles in a moment.

Speculations on reality are part and parcel of man's inherent nature, and perhaps the reality of one's Reality is far less important than the satisfaction it gives. Certainly Mr. Laucks has progressed much further in his thinking than many of us. His thought-provoking discussions are well worth consideration, especially for those scientists who want a stepping stone to the more sophisticated—though often less easily intelligible—works in the field of scientific philosophy.

Frank E. Egler
American Museum of Natural History
New York, New York

A Monograph on Chironomids[1]

This comprehensive volume, the 20th of the series, deals with the life, distribution, and economic importance of the two large dipterous families Chironomidae (Tendipedidae) and Ceratopogonidae (Heleidae). The author, Dr. Thienemann, for many years director of the Hydrobiological Station at Plön, and Professor Emeritus of zoology at the University of Kiel, actively engaged since 1906 in limnological research, presents under the title of *Chironomus* a summary of the work of himself, his colleagues, and of many workers in all parts of the world.

Following a brief historical introduction, there are three sections (or "books") of which the first deals with life history and development, the second with geographical distribution and distribution in accordance with habitat, and the third with the economic importance of the insects concerned.

Of the numerous subjects into which the first section is divided may be mentioned: adaptation to environment, ecdysis, food habits, intersex and the relation to internal parasitism, movement in general, movement at the water surface, parthenogenesis, parasitism by infusoria, mites, molds, etc. The numerous text figures illustrate details of structure of larvae and pupae that will prove of use to the taxonomist. In this connection the author stresses the importance of specific determination of the adult stage of the material studied.

In the second section of this volume numerous types of habitats are discussed, among them bogs, lakes (fresh and salt water), leaf axils of tropic plants, pitcher plants, ponds, pools, springs (cold, hot, mineral, sulphur), and soils.

The third section deals with those species of the families under consideration that are of economic importance. The subject matter of this section is treated under several headings.

a. Noxious species.

Among the noxious species are members of the genus *Culicoides* (Family Ceratopogonidae). These are vicious biters and in some cases are vectors of disease. Their larvae are aquatic. On the other hand the members of the Family Chironomidae are non-biting and mostly innoxious. The larvae of most of these are aquatic, living in pools, ponds, lakes and streams. In some cases they may be found in the city water supply reservoirs, thence in the water pipes and thus occasionally find their way into the drinking water, becoming a nuisance.

b. Chironomids in the effluents of filter beds of sewage disposal plants.

In Europe the Chironomid larva chiefly concerned is *Chironomus thummi* Mg. a species that appears at times in enormous numbers. The presence of the larva and pupa of this form in water serves as an indicator of organic waste matter. In connection with his work on the inland waters of New York, Townes (1945) mentions a species which he calls *Chironomus riparius* Mg. as having similar habits that may be identical with the European *C. thummi* K.

c. Living Chironomid larvae (blood worms) as an article of commerce.

It is surprising to learn that some Chironomids, chiefly *Chironomus thummi* have a commercial value of some importance, some dealers of aquarium supplies, in parts of Europe offering them for sale as food for aquarium fish.

d. Chironomids as significant factors in fishery industries.

That Chironomid larvae and pupae form a very important part of the food of the fish of inland waters is emphasized by the author in an extended review illustrated by many tables and graphs of chemical analyses, temperature data, counts of larvae in the stomachs of fish of streams and lakes, population counts of larvae and pupae of lake and stream bottoms, and other studies of interest to limnologists, fish hatchery superintendents, and students of life in inland waters.

[1] Thienemann, August, 1954. Die Binnengewässer. Vol. 20. Chironomus. XVI + 834 p. Bound. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung. RM 143.50

The book concludes with a comprehensive literature list of 47 pages, a valuable 22 page tabulation of the species of the Chironomidae and Ceratopogonidae mentioned in the text, and a subject-matter index that includes the names of the fish to which reference is made.

As an indispensible reference work this volume will be heartily welcomed by limnologists, ecologists and students of the life in inland waters.

O. A. Johannsen

Department of Entomology
Cornell University
Ithaca, N. Y.

Irrigation Development and Public Water Policy[1]

A readable book, even though one's major interests are not irrigation, socio-economics, and public policies. The kind of book from which ecologists can obtain an objective and well-rounded viewpoint on this extremely important type of land use—in its relation to other land uses; particularly forest, range, wildlife, and watershed uses.

The significance of irrigation in the national economy is increasing so rapidly, particularly in the Great Plains, that textbook statistics are likely to be misleading. Dr. Huffman uses few of them. Quite apart from publicized public projects, are the thousands of new systems installed annually on individual ranches and farms. Private financing has become common since irrigation moved eastward with great increase in pumping systems from wells and streams, often with the new-type sprinkler systems to irrigate on irregular relief. Thus the data in Table 13 indicate approximately 32,000 acres irrigated in Nebraska in 1945. *Nebraska Irrigation Statistics* of 1948 showed approximately one million acres with plans for two and one-quarter million. The latter figures may, by now, be equally obsolete. Also, in Texas the increase through the past ten years has been immense, largely through private pumping of ground-water reserves.

Professor Huffman has not dodged controversial issues; and there are many in his subject. His appraisals of them appear fair to this reviewer. The liberal use of direct quotations from advocates of different philosophies, add interest as well as helping the uninitiated to understand the reasons for current policies and regulations at international, federal, state, and project levels.

The volume reviews past experience in developing irrigated agriculture; considers the varied phases of current developments from planning through organization, financing, and operation; and points up essentials for sound irrigation policy on the local, regional, and national levels.

Ecologists will find discussions of many topics of special interest to them that would scarcely be expected from the title or the preceding summary. Some indicative selected quotes follow: Page 3, "Historically, the development of new irrigation projects has been considered as a problem of . . . the engineers . . . and the individuals who settle on the farm units." Page 3, "The blueprint of the individual farm and its place in the economy are considered to be as important as the blueprint of the dam, the pumping plant, or the canal." Page 121, "Farm operators on irrigated land are faced with the same problems of conservation as other farmers." "Most of the emphasis has been on irrigating new land." Page 152, after pointing out the American penchant for straight lines, the author notes that they ". . . have little in common with the behavior of water." Page 153, ". . . the vital influence of the (watershed) land has often been ignored, perhaps because too many people fail to recognize the inseparability of land and water problems." Page 154, "The land itself still remains the best storage reservoir for water." Page 155, "No one should be more interested in this than the irrigation farmer." Page 173, "There should be no compromise in a program to achieve *physical development* of river basins in accordance with basic land-water relationships. There is, however, considerable latitude in the type of *administrative organization* which can effectuate physical development." On pages 176-189 there is a remarkably analytical treatment of the question, "What is the Public Interest?" The pages 249-285 deal with ". . . the demand for the production from agricultural lands." and ". . . alternatives for supplying the necessary agricultural production."

The book ends with 20 points regarded by the author as the important components of a sound irrigation policy. There is an 18-page bibliography listing references under 17 subject-matter divisions and indexes to both cited names, and subjects.

The author's background in economics and resource planning as well as his current activities with the Missouri Basin Regional Research Committee, and the Missouri Basin Survey Commission qualify him to deal authoritatively with his subject.

[1] Huffman, Roy E. 1953. Irrigation development and public water policy. 336 pp., 5 illus., 14 tables. New York: Ronald Press Co. $6.50.

E. J. Dyksterhuis

5342 Cleveland
Lincoln 4, Nebraska

A Herd of Mule Deer[1]

Another exhaustive mammal study on the California Hastings Reserve brings together a wealth of information on the mule deer. Linsdale and Tomich, together with a score of their colleagues, have once more amassed no end of detail on a single species. This account provides the ambitious reader with details of cervid behavior that cannot be matched elsewhere. Documentation of structure, communication, behavior, habitat, reproduction, food and other matters are faithfully recorded as observed over a 13 year period.

No study of any cervid has been made in greater detail. Throughout this detailed report the many notes show little editing. The study may well be the despair of those who look for explanations of why the deer do this or that. Perhaps this is the manner in which we all

[1] Linsdale, Jean M. and P. Quentin Tomich. 1953. A herd of mule deer. 576 pp., 171 figs. Berkeley: Univ. California Press. $8.50.

should write. Unfortunately or otherwise, an open sesame to excess pagination is not available to most authors. Is it well that any institution should foster the details included by the authors of this report? Would justified editing have dismissed the useless figures (pp. 156-157) of the deer in its various attitudes? Do such illustrations add to the value of a report? I think not.

A commendable trait of the ecologist is to record, in sufficient detail, observations made on the spot. Behavorial traits are often ephemeral; an observation once made may not be duplicated in a lifetime of study. In his "Key to North American Birds," Elliott Coues made a few remarks that all naturalists should take cognizance of. "Don't trust your memory, it will trip you up; what is clear now will grow obscure; what is found will be lost. Write down everything while it is fresh in your mind, write it out in full; time so spent now will be time saved in the end, when you offer your researches to the discriminating public . . . write as if a stranger were looking over your shoulder." Coues set an exemplary example, but he used good judgment in not recording the minutia in his published works. It is important that the record of natural phenomena make an effort to condense the raw data into a succinct review of the field observations. This is important to all who would digest the material with a modicum of effort.

Every serious student of cervid behavior will be aware of the major contribution included in this study. The social structure and behavior of this deer group will be of considerable interest to those interested in animal behavior if he can interpret the many specific data which are presented. Exact details are provided on the plants utilized by the mule deer; one might wish further comment regarding specific seasonal utilization. For the deer, like our tree squirrels, are for the most part profligate feeders, selecting many species with seasonable abandon. A 65 page chapter deals with reproduction. One might wish more on the uterine life of the fawn than that "gestation lasts for about seven months." The swollen belly of the doe carries many ecological secrets. Such a study might well have supplemented the observed facts and added measurably to the important phases of the deer's ecology. Elsewhere the point is made that when favorable food is limited, the deer population declines. No instance in this herd suggests that the population exceeded its food supply, a situation that has occurred so often in deer herds.

While the jacket announces that full field records were subjected to analysis and interpretation by the authors, little appears on the interpretation of these recorded data. A summation, developed in several pages, would be most useful to the inquisitive reader.

Jean Linsdale and his colleagues will probably continue to record the details of their studies on yet more species of this localized area. Perhaps those of us who are asked to comment on these studies are remiss; perhaps we too might wish to emulate this industry and good fortune in living daily with the animals he knows so well. Few, if given such an opportunity, would match his meticulous efforts. We wish only that this accomplished naturalist would summarize his detailed labors and make the results readily accessible to the many who wish interpretation of recorded observation.

W. J. Hamilton, Jr.
Department of Conservation
Cornell University
Ithaca, New York

Growth and Differentiation in Plants[1]

The problems of growth and differentiation are of interest to all biologists. The present volume is a monograph of the American Society of Plant Physiologists and sets out to give "a critical evaluation of the present status of the various topics." To the extent that it permits workers in allied fields to obtain readily an outlook upon the trend of botanical thought upon these great problems, the book will commend itself.

The book suffers from a parochial approach. The all-embracing problems with which it deals are limited neither to a society nor to a country. Of the 18 chapters by different authors, only 2 originate from workers who are not of the U.S.A. The continent of Europe is not represented in the list of authors. The University of Iowa is represented in 5 chapters.

The different chapters are very variable in content, style and the authority of the presentation. Some, as, for example, the one dealing with differentiation in shoot and root axes, are admirably comprehensive and authoritative in their treatment. The all-important subject of plant morphogenesis is represented by a very general essay, supported neither by citations nor by detailed references to specific observations. Though this may be interpreted as a useful extension of the introductory chapters, which is itself almost an epitome of the book, it still leaves the work lacking in any formal and comprehensive treatment of morphogenesis. For such a comprehensive treatment, the reader must turn elsewhere. The chapter on Growth Correlations cites 120 references, of which 15% are to foreign sources. Of the latter, ½ are references to journals in English. It is doubtful whether the U.S.A. as yet has this degree of monopoly on scholarship in this broad area of botanical science. Although much has been done to interpret the role of the root in relation to its growth and development, the chapter on this subject is curiously patchy. The highly significant work of Brown (R) manages only to obtain notice as one of a group of 7 omnibus references, and thereafter the chapter proceeds almost as though this work had not been done. There are also other obvious omissions.

Ecologists interested in the growth of populations may well be interested to learn about the mathematical analysis of plant growth. The brief elementary chapter on this subject makes no reference to the literature in this field, and certainly makes little demand on mathematical comprehension. Nor does it solve any problems. Ecologists will naturally turn to such chapters as those on dormancy, photoperiodism, vernalization, and the related chapters which deal with the various ways in which the growth of plants is subject to hormonal regulation. The chapter on dormancy, with its obvious parallels throughout the animal kingdom, is narrow in the extreme. It refers to only 10 references, of which 8 are from the Boyce Thompson Institute. Admirable as these may be,

[1] Loomis, W. E. (Editor) 1953. Growth and differentiation in plants. v + 458 pp., 45 figs., 8 plates. Ames: Iowa State College Press. $7.50.

workers in other fields of biology should not imagine that work and thought in this area are as restricted as this might lead one to suppose. The other chapters on flowering and fruiting, horomonal regulation, etc., are among the most interesting in the book.

In short, ecologists will naturally be attracted by the subject matter of this book, in which they ought to find much of interest. They should not expect, however, that it will be authoritative, or even fully informative, at all the points which will arouse their interest. Collective works are a feature of the times—perhaps the only solution to adequate coverage of the rapidly expanding biological literature. Since individual authors, are, in this way, spared the responsibility of covering the whole field, one ought to be able to look to editors and authors alike to ensure that the individual chapters are reasonably comprehensive, and that the work has some unity of plan. In this respect, the volume has obvious shortcomings.

F. C. Steward

Department of Botany
Cornell University
Ithaca, New York

Geologic Time and Evolution[1]

During the last half-century measurements of the duration of geologic time based on radioactive elements have provided a few fixed points here and there in the stratigraphic column. Plotting of paleontological data against this scale makes it evident that "biological time" is not constant, and that rates of evolutionary change and rates of speciation have more or less consistently decreased in higher and higher groups of organisms—mammals evolving more rapidly than molluscs, for instance.

This little book is an expanded version of a lecture given by Professor Schindewolf on taking his chair a few years ago at the University of Tübingen. It embodies some of the ideas on evolution put forth previously by him in less general works, and some new ones. After dealing with the general problem of the establishment of the geologic column and its subdivision, and methods of dating from uranium to tree rings, he analyzes available data on the probable duration of the paleontological zones, from the 4,000,000 year trilobite zones of the Cambrian to the 300,000 year ammonite zones of the Jurassic, and on the time duration of taxonomic categories from order to species. The last, in general, confirms the concept that "biological time" has shortened, so to speak. "Explosive evolution" is briefly examined, together with questions of patterns of phylogeny with relation to time. Schindewolf no longer emphasizes his earlier ideas, so much criticized, on the sudden appearance of larger groups by macroevolution or typostrophism. In the last chapter he reviews the oft-made suggestion of a direct relation between earth movements and evolutionary spurts, and concludes that "organic evolution is not a reflection of movements of the earth's crust."

[1] Schindewolf, O. H. 1950. *Der Zeitfaktor in Geologie und Paläontologie.* 114 p., 18 figs. Schweizerbart'sche. Stuttgart. Paper, $2.30.

John W. Wells

Department of Geology
Cornell University

Social Insects[1]

The social insects exhibit extreme group integration and division of labor and will always be of special interest to the biologist who attempts to understand these important principles of life. Because of the parallels in social behavior, the layman sees a fascinating similarity in the social systems of insects and men. Richards has written a book designed to present some of the more modern studies to the interested layman whose knowledge of biology and entomology is elementary and whose vocabulary is nontechnical.

The literature of the last few decades is not very fully digested, although some interesting new studies have been sampled. The approach is scientific and is notably free from anthropomorphisms. Portions of the conclusions are sound, but there are many statements that indicate a lack of critical judgment based upon personal knowledge of the subject matter. For example, the chapter on the wasps is much better than that on the termites because the author has personally studied wasps much more extensively and intensively.

The book has little value for the professional biologist, but will interest the intelligent layman. The illustrations, particularly the photographs, are good. A few of the figures are poor, for example the modification of Escherich's erroneous illustration of the termites in a royal chamber. The philosopher of social systems should not take some of the conclusions too seriously.

[1] Richards, O. W. 1953. The Social Insects. 219 pp., 12 text figs., 51 photographs. London: MacDonald. New York: Philosophical Library. $4.75.

Alfred E. Emerson

The University of Chicago